2000

Microhabitat selection by the amphipods Echinogammarus ischnus and Gammarus fasciatus in laboratory and field experiments.

Colin David Alexander. van Overdijk
University of Windsor

INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

ProQuest Information and Learning
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
800-521-0600

Microhabitat selection by the amphipods Echinogammarus ischnus and Gammarus fasciatus in laboratory and field experiments.

by

Colin D. A. van Overdijk

A Thesis
Submitted to the Faculty of Graduate Studies and Research
through the Great Lakes Institute for Environmental Research
and
the Department of Biological Sciences
in Partial Fulfillment of the Requirements for the Degree of

Master of Science

at the University of Windsor
Windsor, Ontario, Canada

2000

Abstract

The Ponto-Caspian amphipod Echinogammarus ischnus was first detected at a lone site in the lower Detroit River in 1995, and has quickly spread through the lower Great Lakes. Analysis of archived samples revealed that Echinogammarus was present in the western basin of Lake Erie at Middle Sister, East Sister and Pelee Islands during June 1994. Moreover, body length sizes classes demonstrate that Echinogammarus was a fully reproducing population with different generations at the time of collection in 1994, and that it most likely invaded Lake Erie no later than 1993.

It has been suggested that it is displacing the native amphipod Gammarus fasciatus and that replacement of amphipod species could have far-reaching implications. However, no mechanistic studies have been conducted in the laboratory or field to assess habitat preference by invading Echinogammarus, or its effects on resident Gammarus populations. Thus, the invasion of Lake Erie by Echinogammarus provides an excellent opportunity to explore interspecific interactions between resident and invading amphipod species. Laboratory and field experiments reveal the interaction between these two species is neutral over short time periods, commensal over brief periods, and negative over longer periods due to abundance patterns of each species. Biomass of Cladophora encrusted on rocks had no effect on Echinogammarus abundance, but it did have positive effects on Gammarus' abundance. Echinogammarus abundance was positively affected by Dreissena-encrusted biomass, while Gammarus abundance fluctuated on Dreissena-encrusted biomass. Thus, introduction and spread of Dreissena in the Great Lakes appears to have facilitated Echinogammarus' colonization, establishment and dispersal in a manner consistent with Simberloff and Von Holle's 'invasional meltdown' hypothesis.

Acknowledgements

My most sincere gratitude goes out to the following people who have made this thesis possible and have helped in its completion. First and foremost, to Dr. Hugh MacIsaac who had the strength and courage to take me on as a graduate student. Hugh saw past the fact that I had been out of school for six years, since completing my bachelors, and was a little rusty in the world of academia. His patience, insight and guidance throughout my thesis and graduate career have made me a better researcher, and person.

I am deeply indebted to Dr. Igor Grigorovich, whose knowledge on Ponto-Caspian species has greatly enhanced the quality of this thesis, and my knowledge of exotic species from this region. His help in the laboratory and field experiments aided in the completion of this thesis and will never be forgotten.

I would also like to thank my committee members Dr. Al-Aasm, Dr. Haffner and Dr. Weis for providing constructive ideas and comments throughout my research.

I also need to thank those that have helped me along the way. People like Jason Postill that worked tirelessly with me in the field, and to Tracy Mabee and Emily Awad that endured many monotonous hours of measuring, and 'cleaning' zebra mussels.

I need to acknowledge some close and dear friends, my comrades in arms, which were pivotal in making my time here enjoyable: Dean Fitzgerald, Karen VanSteelandt, John Burt, Scott Peters, Jocelyn Gerlofsma and Lawrence Heidinga. Irrevocably, Mark Whelly and Denis Roy were there for me when I needed them the most. *On y va Athos et Porthos.*

Finally and perhaps most importantly, my appreciation goes to those that I care about the most. My mother Judy, for all of your generous support and encouragement through the tough times, my brothers Troy and Ryan, my sister-in-law Jackie, my niece Madison, and to my nephew Jesse, for always being there. Last, but not at all in the least, to Julius Xavier.

Voor mijn familie en de
Koninklijke Nederlandse Voetbal Bond.

Table of Contents

List of Figures

Temporal Survey at Middle Sister Island

Laboratory experiment of habitat preference

Field Colonization Experiment

List of Tables

Temporal Survey at Middle Sister Island

Laboratory experiment of habitat preference

Field Colonization Experiment

Background

Background

"It spread beyond England very speedily. Soon in America, all over the continent of Europe, in Japan, in Australia, at last all over the world, the thing was working towards its appointed end."

This quotation from H.G. Wells' "The Food of the Gods" has an ominous overtone, that of an organism originating from a single area, expanding, then spreading all over the world to a destructive "appointed end".

Exotic species are organisms that arrive and establish in new host regions where they never existed before. An invasive species is an exotic species that experiences explosive population growth within its new range, often with catastrophic ecological or economic effects. Although they may not all be destructive or harmful, invading species follow the general pattern of colonization, establishment, reproduction and population growth.

Range expansion by exotic or invasive species may occur intracontinentally or intercontinentally, in aquatic or terrestrial habitats. In his book "The Ecology of Invasions by Animals and Plants", Charles Elton focused primarily on invasive species. In this chapter, I address Elton's and other researchers' concepts pertaining to species invasions. I then examine species invasion patterns in the Great Lakes, and focus specifically on patterns of amphipod introductions.

Elton's (1958) volume was one of the first to focus attention on effects humans have on natural habitats *via* the introduction of invasive species into new habitats. Humans facilitate the movement of plants, animals and microorganisms across biogeographical realms that the species could never surmount naturally. In fact, many of the most successful exotic species are those that have developed commensal associations with man

(Elton 1958, Ehrlich 1989, Lodge 1993). For example, species of birds and plants were brought to New Zealand and other British colonies by 'acclimatization societies' so that people would feel more 'at home' (Elton 1958). However, not all exotic species are intentionally introduced; many are introduced accidentally and many introduced species fail to establish. Moreover, only a small proportion of exotic species explode in population density and spread very rapidly to become invasive species (Elton 1958). Indeed, Williamson and Fitter (1996) stated that only 10% of species that invade a new area establish successfully, and only 10% of these increase in density to the point that they become pests (i.e. invasive).

Elton (1958) suggested that invading organisms work themselves into simple systems, and that most invasions occur on cultivated lands or those otherwise modified by humans. These 'disturbed' areas were presumed simpler in character and easier to invade compared to richer, more complex systems because they generally contain fewer predators, competitors and other enemies (Elton 1958, Lozon and MacIsaac 1997). Crawley (1986) also proposed that invasive species move into disturbed areas because intensity of predation and competition tends to be reduced.

There are generally between 10^2 and 10^4 established introduced species in most countries (Lodge 1993). These biological invasions pose a threat to ecological communities and to global biodiversity by displacing native species (Lodge 1993). Introduced species may cause extinctions of native species *via* competition, predation, or restriction of ecological ranges (Vermeij 1996). Some workers have argued that the species introduction problem is resulting in homogenization of the world's biota (Lodge 1993, Lodge *et al*, 1998).

Ecological theory predicts a number of features common to exotic species and to invaded habitats. Traits common among exotic species include but are not limited to: large native ranges, high abundance in native range, catholic diets, short generation times, vegetative or asexual reproductive capability, r- strategist life history, and an ability to function under a wide range of physical conditions (Crawley 1986, Ehrlich 1989, Lodge 1993, Ricciardi and Rasmussen 1998). Features that render areas susceptible to invasions are thought to include a climatic match between donor and recipient habitats, absence of natural predators, and a low diversity of native species (Lodge 1993). A combination of these factors has been proposed to affect the success of exotic species (Ehrlich 1989). The two leading causes of failed introductions are weather and predation, though other factors such as competition and disease may also cause invasions to fail but are difficult to quantify (Lodge 1993). Unfortunately, much more is known regarding successful invasions than unsuccessful ones, thereby limiting our overall understanding of invasion biology.

Crawley (1986) suggested that body size of animals influences invasion success and is positively correlated with competitive ability through interference capability, but negatively correlated with intrinsic rate of increase. He also reported that the lack of natural enemies and habitat refugia were important determinants of success (Crawley 1986). Refugia can provide enemy and/or competition free-space and may provide protection from extremes in environmental conditions (Crawley 1986).

Arrival, colonization, establishment and integration are the sequential processes of invasion that must occur for species to invade successfully (Vermeij 1986). Genetic attributes of invading species can also play a role in establishment success (Barrett and

Richardson 1986). Invading populations are usually established by a small number of immigrants, potentially resulting in a loss of genetic variation (Barrett and Richardson 1986). However, the scale of this problem depends on the size of the original population, availability of new recruits, and how long the population remains small (Barrett and Richardson 1986). This problem can be overcome by the parameters mentioned above (i.e. a high rate of intrinsic increase, short generation times) that facilitate rapid population growth (Crawley 1986, Ehrlich 1989).

Some environments are assumed to be more successfully invaded than others (Lodge *et al.* 1998). Aquatic environments may be easier to invade than their terrestrial counterparts for two reasons related to human use (Lodge *et al.* 1998). First, huge numbers of individuals from many pelagic and benthic taxa are transported out of their normal range *via* movement of ballast water by intercontinental ships, in fish bait buckets, in wells of boats, fouled on boat trailers and hulls, or by releases from aquaria and water garden practices (Lodge *et al.* 1998). Secondly, once introduced, dispersal may be easier for freshwater than terrestrial species because fewer dispersal barriers exist between source and donor ecosystems (Lodge *et al.* 1998). Indeed the movement of water itself (i.e. waves in lakes and flowing water in streams and rivers) aids in the dispersal of species to new locations (Lodge *et al.* 1998).

In North America, the Great Lakes are host to many established exotic species, with at least 145 identified (Ricciardi and MacIsaac 2000). Since the 1800's, immigrating Europeans brought with them a host of exotic species. Indeed, 55% of the exotic species in the Great Lakes are from Europe, with another 13% originating from the Atlantic coast of North America (Mills *et al.* 1993). Over one-third of these species have arrived since

the opening of the St. Lawrence Seaway in 1959 (Mills *et al.* 1993). Most of the introductions have arisen from unintentional releases (29%) and from ships (29%), of which 63% and 31% of the latter were from liquid and solid ballast, respectively (Mills *et al.* 1993). Ballast water has brought many pest species to the Great Lakes, including the zebra mussel Dreissena polymorpha.

Pest species cause major ecological and economic damage to industries and utilities at a cost of 120 billion dollars per year in the United States alone (Mills *et al.* 1993, Pimentel *et al.* 2000). Thirteen species discussed by Mills *et al.* (1993) have substantially influenced the Great Lakes either ecologically or economically; most of the other introduced species in the Great Lakes have had little or no ecological or economic impacts.

The Great Lakes have been invaded by more exotic species since Mills *et al.* (1993) published their paper. These include two species of amphipod Echinogammarus ischnus (Witt *et al.* 1997) and Corophium mucronatum (Grigorovich and MacIsaac 1998) and the fishhook waterflea Cercopagis pengoi (MacIsaac *et al.* 1999). The most recent introduction reported is by the diatom Thalassiosira baltica in Lake Ontario (Edlund *et al.* 2000).

Amphipods exhibit many of the traits of successful invaders, and are spreading throughout many parts of the world (Chapman 1988). For example, Corophium curvispinum invaded and experienced a population explosion in the River Rhine, since its colonization in 1987, achieving maximum densities of 100,000-750,000 Ind./m^2 (van den Brink *et al.* 1991, den Hartog *et al.* 1992, van den Brink *et al.* 1993). These amphipods also showed a remarkable range extension. They first appeared in the middle Rhine and a

year later were in the lower Rhine, a distance of about 200-500 km (van den Brink *et al.* 1991). Corophium curvispinum increased explosively because it can produce up to three generations per year from April through October (van den Brink *et al.* 1991, den Hartog *et al.* 1992, van den Brink *et al.* 1993). Other conditions responsible for its success include a decline in the native macrozoobenthos due to anthropomorphic changes, and favourable biological and ecological conditions in the Rhine system (den Hartog *et al.* 1992). Corophium constructs and lives within mud tubes (van den Brink *et al.* 1991), and large populations on the river bottom have smothered Dreissena beds (den Hartog *et al.* 1992, Rajagopal *et al.* 1997). The River Rhine was also colonized in 1995 by another Ponto-Caspian amphipod, Dikerogammarus villosus (bij de Vaate and Klink 1995).

The River Rhine is not the only system experiencing drastic changes in amphipod populations. With the addition and formation of many canals in the former Soviet Union to aid in shipping, many Gammarus spp., Chaetogammarus spp., Dikerogammarus spp., and Pontogammarus spp. have invaded or increased in abundance in European rivers such as the Danube, Dniester, Dneiper, Don and Volga (Jażdżewski 1980). These increases were due primarily to human activities, including intentional stocking (Jażdżewski 1980).

Europe is not alone in experiencing amphipod invasions. The Pacific West Coast of North America from areas south of San Francisco Bay north to Washington state have been invaded by Ponto-Caspian, Asian and Atlantic amphipod species (Chapman 1988).

The Great Lakes have been invaded primarily by Ponto-Caspian species in recent years, including mollusks, fish, waterfleas and amphipods (Mills *et al.* 1993, Ricciardi and Rasmussen 1998, MacIsaac and Grigorovich 1999, Ricciardi and MacIsaac 2000). The Great Lakes are vulnerable to invasion by as many as 17 additional Ponto-Caspian

species, many of which could have significant ecological impacts (Ricciardi and Rasmussen 1998, Ricciardi and MacIsaac 2000). These include one species of polychaete, five mysids, one bivalve and three fish species (Ricciardi and Rasmussen 1998). The remaining seven species (41%) are amphipods, two each from the genera Corophium, Dikerogammarus and Pontogammarus and one species of Obesogammarus (Ricciardi and Rasmussen 1998). Amphipods may be good candidates for invasion owing to their relative under-representation amongst Great Lakes fauna. Ponto-Caspian amphipods, in particular, might invade successfully considering their success in invading ecosystems elsewhere in the world (Jaźdźewski 1980, Crawley 1986, den Hartog *et al.* 1992).

The success of invading amphipods in the Great Lakes may be due to size differences between exotic and native species. One genus that is native to the Great Lakes, Hyalella, is considerably smaller than both G. fasciatus and E. ischnus. Since body size is positively correlated with competitive ability (Crawley, 1986), Hyalella might be competitively suppressed by other larger amphipods, including invading Echinogammarus.

Many of the hypotheses presented heretofore remain untested. The overall objective of this thesis is to address habitat preferences of, and interactions between, native and exotic amphipods in Lake Erie. The invasion of Lake Erie by Echinogammarus provides an excellent opportunity to explore interspecific interactions between resident and invading species.

The following chapters utilize laboratory and field experiments to explore habitat preferences for the primary amphipod habitats available in Lake Erie, namely bare rock

and Cladophora- and Dreissena-encrusted rocks. Specific hypotheses that were tested include: 1) amphipod species have no preference for complex substrates (e.g. Cladophora- or Dreissena-encrusted rocks) over simple ones (bare rock); 2) amphipod habitat preferences are not affected by the presence of other amphipod species; 3) colonization and occupation of rocky substrates in Lake Erie are not affected by habitat quality or by lake depth.

Temporal Survey at Middle Sister Island

Introduction

The threat of exotic species, an issue of global concern, has become more prevalent in the 20th century due to increased shipping activities and human travel (e.g. Elton 1958, Carlton and Geller 1993). Exotic species have invaded all parts of the globe and all types of ecosystems, and have caused important conservation problems (Carlton and Geller 1993, Ruiz *et al.* 1997, Goodwin *et al.* 1998). Exotic species are the second biggest cause of biodiversity loss in the United States following habitat destruction (Enserink 1999). Exotic species are a threat economically and ecologically, and are causing a homogenization of the Earth's biota (Lodge 1993). In the United States alone, exotic species cause environmental damage totaling more than $ 138 billion per year (Pimentel *et al.* 2000).

Classic invasion theory was developed in Charles Elton's (1958) volume 'The ecology of invasions by animals and plants' and dealt mainly with attributes of invading species and those of invaded habitats. Species attributes include: 'r'-selected traits, high genetic variability, high dispersal rates, a broad diet, human commensalism, and many other characteristics (Elton 1958, Lodge 1993). Characteristics of invaded habitats include, but are not limited to: disturbance, low diversity of native fauna, and a climatic match between host and native habitats (Lodge 1993).

Elton (1958) also proposed the 'biotic resistance' model. This model suggests that ecosystems rich in native fauna will resist or repel new invaders due to highly efficient utilization of available resources, while ecosystems depauperate in fauna will be more vulnerable to invasion (Enserink 1999).

Modern invasion theorists have dispelled most of these concepts pertaining to species attributes and habitat characteristics. A current theory is based on concepts of propagule pressure and 'invasion corridors', i.e., a route and associated mechanism(s) that aid the long-distance dispersal of numerous species or their various life stages to new biogeographic realms (see MacIsaac *et al.* 1999). Aquatic corridors have been proposed that link the transfer of ballast water (and species) between Asian ports and San Francisco Bay, (Cohen and Carlton 1998, Zhang and Dickman 1999) or Australia (Jones 1991). Likewise, invasion corridors have been proposed between Europe and North America. For example, MacIsaac *et al.* (1999) and Ricciardi and MacIsaac (2000) postulated that many of the current exotic species in the Laurentian Great Lakes arrived from the Ponto-Caspian basin (Caspian Lake, Black and Azov Seas) *via* one direct and two indirect routes.

Another new invasion theory proposes mutual, commensal or facilitative interactions between exotic species in recently invaded habitats. Simberloff and Von Holle (1999) examined 254 articles that involved positive, neutral, commensal, or negative interactions between exotic species and discovered that many exotic species facilitate subsequent invaders, a term coined 'invasional meltdown'. Species interactions facilitate invasions by an increase in the chance of survival of a newly invaded species by earlier invaders (Simberloff and Von Holle 1999). Therefore, there is acceleration in the accumulation of exotic species instead of a deceleration as stated in the 'biotic resistance' model (Simberloff and Von Holle 1999). For example, when the zebra mussel (Dreissena polymorpha) invaded the Laurentian Great Lakes in the mid 1980's, it invaded various habitats and eventually became an 'ecological engineer', or 'keystone species' of the

benthos (see MacIsaac 1996a). Establishment of Dreissena spp. had strong effects on benthic fauna, most of which were positive. Species of chironomids, ostracods, snails, hydroids, gastropods and Turbellaria all showed marked increases in abundance with the arrival of Dreissena due to enhancement of habitat availability amongst mussel shells (Griffiths 1993, Botts *et al.* 1996, Ricciardi *et al.* 1997, Stewart *et al.* 1998a, Bially and MacIsaac 2000). To a lesser extent, production of feces, pseudofeces and accumulating organic matter by Dreissena provided invertebrates with an enhanced food supply (Griffiths 1993, Dermott *et al.* 1993, Stewart and Haynes 1994, Wisenden and Bailey 1995, Botts *et al.* 1996, Ricciardi *et al.* 1997, Stewart *et al.* 1998a, Bially and MacIsaac 2000). Amphipods, specifically Gammarus fasciatus, increased tremendously following the arrival of Dreissena. For example, Griffiths (1993) reported that G. fasciatus abundance increased from 80 to 400 Ind./m^2 on the north shore, and from 520 to 3,580 Ind./m^2 along the south shore of Lake St. Clair following Dreissena polymorpha establishment. Likewise, Stewart and Haynes (1994) reported that G. fasciatus increased from 233 to 1,670 Ind./m^2 in Lake Ontario, while Dermott *et al.* (1993) found it increased from 1,146 to 24,114 Ind./m^2 in Lake Erie.

It is uncertain whether Gammarus is native or was introduced to the Great Lakes through solid ballast, due to its disjunct distribution (Chace *et al.* 1959, Mills *et al.* 1993); however, Weckel (1907) reported its distribution from Lake Superior to the Hudson River, and as far south as Florida. Thus, given its immense distribution and presence in the Great Lakes in the early 1900's, it will be regarded as 'native' through this study (see Appendix for a picture of Gammarus and life history characteristics).

It has been suggested that the arrival, and subsequent establishment of Echinogammarus ischnus, an amphipod native to the Ponto-Caspian basin, has been facilitated by Dreissena since the former was initially discovered in the lower Detroit River in 1995 (Witt *et al.* 1997, A. Ricciardi, pers. comm.).

Echinogammarus displayed rapid range extension, spreading beyond the Caspian Sea into the Volga, Dneiper, and Vistula Rivers in the early 1960's (Mordukhai-Boltovskoi 1964), into the Don, Dniester and Danube Rivers in the 1980's (Jaźdźewski 1980), and finally reaching the Netherlands *via* the lower Rhine in the early 1990's (van den Brink *et al.* 1993). Its spread in the Great Lakes has also been rapid, as it has expanded from a single site in the lower Detroit River to Lake Huron, through Lakes Erie and Ontario and into the St. Lawrence River (Dermott *et al.* 1998). Recently it was detected in Lake Michigan (T. Nalepa, pers. comm.; see Appendix for a picture of Echinogammarus and life history characteristics).

In this study, I examine temporal changes in abundances of exotic and native amphipods in Lake Erie. Specifically, I utilize a combination of archived and newly collected samples to examine relative distributions and abundances of Echinogammarus ischnus and Gammarus fasciatus on a variety of habitat types near an island site in western Lake Erie. A further purpose of this study was to establish the date of Echinogammarus invasion into the Great Lakes. Specific hypotheses examined in this chapter include:

1) Echinogammarus ischnus was not present in Lake Erie prior to its initial discovery in 1995;

2) amphipod species have no preference for complex substrates (e.g. Cladophora- vs. Dreissena-encrusted rocks) in nearshore habitats;

3) amphipod abundance is not affected by the presence of other potentially competing amphipod species;

4) colonization and habitation of rocky substrates are not affected by lake depth.

Materials and Methods

1994 Lake Erie Amphipod Survey

Archived samples were assayed to determine whether Echinogammarus was present prior to 1995. Samples were collected in June 1994 at various sites in the western basin of Lake Erie using a petite Ponar grab and a 600-μm-sieve bucket. Samples were collected by Dr. J.J.H. Ciborowski. Additional rock samples were hand-collected *via* snorkeling at Middle Sister, East Sister and Pelee Islands during summer 1994. Fauna collected were fixed in 5% Kahle's solution, passed through a series of sieves (4 mm, 1 mm, 500 μm, and 250 μm), and separated into dense and buoyant matter by the 'gold panning technique' (Ciborowski 1992). Fauna were sorted by order and stored in 70% ethanol.

Identity of collected amphipods was re-analyzed in spring 1998 using descriptions from Witt *et al.* (1997). Samples were processed under a dissecting microscope (Zeiss Jena, model Technival 2) at 5X magnification, counted, and preserved in 5% sugar-formalin solution. Total body length measurements of Echinogammarus (tip of rostrum to end of telson) were assessed using a dissecting microscope (Leica Wild M8) at 6X

magnification. Images were outputted *via* a video camera and framegrabber to image analysis software (Optimas Version 6.2) on a Dell XPS D300 personal computer.

Middle Sister Island Amphipod Survey

Analysis of the amphipod community was conducted by using archived (1995-96) and newly-collected samples (1997-98) adjacent to Middle Sister Island, a small dolomite outcrop approximately 15.7 km from the Canadian mainland in the western basin of Lake Erie (Fig. 1) (for more information see MacIsaac 1996b).

Sample collection

During June 1995 and 1996, four transects were fixed perpendicular to shore, two each on the west and east sides. Six rocks encrusted with Dreissena were collected by SCUBA at each of five different depths (0.9, 1.5, 1.8, 2.7 and 3.6 m), sealed underwater in polypropylene bags (large Ziploc® freezer bags), and brought to the surface and fixed immediately in 5% Kahle's solution. In 1996 only three transects were surveyed (one on the west and two on the east). The exact depths that the rocks were collected from were not recorded, thus all depths from 1996 are categorical with 1 being the shallowest and 5 the deepest. The same sampling technique was used in 1997 and 1998; however, there were differences in the time of collection, types of rocks gathered, and depths sampled. Rocks were collected in August (late summer) instead of June (early summer) along each of the same three transects where rocks were collected in 1996. Five Dreissena-encrusted rocks were collected (instead of six as in 1995 and 1996), plus an additional five Cladophora-encrusted rocks at each of the five depths. In 1997, depth was not

standardized along each of the three transects, thus rocks were collected from various depths along each transect. However, in 1998 five depths were standardized (0.5, 1.0, 1.5, 2.0 and 2.5-m) along each of the three transects, and five rocks encrusted with Dreissena or with Cladophora were collected at each depth. In 1997 and 1998, rocks were fixed in 5% sugar-formalin instead of 70 % ethanol, which was used in 1996. (See Table 1 for a review of sampling methods and techniques from the different years.)

Sample processing and identification

In the lab, all rocks were scraped clean with a surgical blade, with biota placed in separate, marked jars and preserved in either 70% ethanol (1995) or 5% sugar-formalin solution (1996-1998). Fauna were separated using the 'gold panning technique' described above and preserved in 70% ethanol (1995) or 5% sugar-formalin solution (1996-1998). Amphipods collected were analyzed in the spring of 1998, identified and sorted using descriptions from Witt *et al.* (1997), under the dissecting microscope at 5X magnification, counted, and preserved in 5% sugar-formalin solution. In 1995 and 1996, rock surface area was calculated by the mass of aluminum foil required to cover the rock and the area per unit mass of the foil. Volume of rocks was assessed using the water displacement technique in 1997 and 1998, with three measures taken for each rock. Volume of rocks was then converted to area (square centimeters) from surface area-rock volume correlations calculated by MacIsaac (1996b). Dreissena samples were cleaned by removing broken shells and byssal threads, sorted by species, blotted dry, and wet mass recorded on an AND FX-200 electronic balance. In 1997 and 1998, Dreissena dry weight was determined by placing mussels on pre-weighed, dried aluminum boats in an

oven for 48 hours at 60° C. Cladophora wet weight was determined on the electronic balance after filaments were compressed between paper towels to remove excess water.

Statistical Analyses

To assess whether rock area varied among the years and its possible effect on amphipod abundance, variation in rock area was determined by 2-way ANOVA with rock area as the dependent variable, year and depth as independent categorical variables, with a year × depth interaction effect included in the model.

To determine whether substrate biomass varied between years, separate 2-way ANOVA's were conducted for both Cladophora and Dreissena treatments. Corrected wet weight biomass (biomass divided by rock area) was the dependent variable, while year (1995-1998) and depth were categorical variables. Year × depth interaction effects were also included in the model. The model was run twice, first for Cladophora biomass in 1997 and 1998 only, and then for Dreissena biomass for 1995 through 1998.

Amphipod abundances for both species were divided by the rock area on which they were present, and log (x + 1) transformed prior to analysis in Systat (Version 8.0). A multiple analysis of variance (2-way MANOVA) was conducted to determine the effects of year and depth on amphipod species abundances on Dreissena substrate. Transformed amphipod abundances of Echinogammarus ischnus and Gammarus fasciatus were entered as dependent variables, year (1995-1998) and depth as independent categorical variables, with a year × depth interaction effect included in the model.

Further MANOVA's were utilized to determine the effects of sampling year on amphipod abundances. The years 1995-1996 and 1997-1998 were grouped together as sampling technique and substrates gathered were comparable within each group. In 1995-1996, transformed amphipod abundances were entered as dependent variables, year and depth as independent categorical variables, and a year × depth interaction effect included in the model. In 1997-1998, transformed amphipod abundances were entered as dependent variables, and year, depth and substrate as independent categorical variables. To determine if amphipod abundances varied with year, substrate and depth, year × depth and substrate × depth interaction effects were included in the model.

To determine effects of rock area and biomass encrusted on rocks on amphipod abundance, separate multiple linear regressions were conducted for each species. Transformed abundances of each amphipod species, corrected for rock area, were entered as the dependent variable, and rock area or Cladophora and Dreissena total wet weight biomass corrected by rock area, entered as an independent continuous variables.

Results

1994 Lake Erie Amphipod Survey

Analysis of archived samples revealed that Echinogammarus was present in the western basin of Lake Erie at least a year prior to its initial discovery by Witt *et al.* (1997) in 1995 (Fig. 1). Echinogammarus was rare in the Ponar grab samples, but was common among the rock samples retrieved from Middle Sister, East Sister and Pelee Islands during June 1994. Echinogammarus abundance was lower than that of Gammarus across

all sites, with its highest abundance occurring at East Sister Island (Fig. 2). The rank order of Echinogammarus abundance in the western basin of Lake Erie from 1994 was East Sister Island, Pelee Island and Middle Sister Island. This suggests that the possible inoculation site of this amphipod occurred between East Sister and Pelee Islands near the Pelee Passage.

Body length size classes from 1994 samples demonstrate that Echinogammarus was a fully reproducing population with different generations, and suggest that the species likely arrived prior to 1994 (Fig. 3).

Middle Sister Island Amphipod Survey

Substrates

Rock area differed between the four years of study ($F = 374.61$, $df = 3, 480$, $p < 0.001$), by depth ($F = 4.45$, $df = 4, 480$, $p = 0.002$), and by year × depth interactions ($F = 2.24$, $df = 12, 480$, $p = 0.010$). Rock areas were larger in 1996, 1997, and 1998 than in 1995 (Bonferroni's test). Rocks were smaller in 1997 and 1998 compared to 1996, and were smaller in 1998 than in 1997 (Bonferroni's test). Rocks were also larger at the third depth than at the shallowest depth (Bonferroni's test). Thus, the rank order of rock areas collected from largest to smallest was 1996, 1997, 1998, and 1995.

Cladophora biomass encrusted on rocks did not vary between 1997 and 1998 ($F = 0.25$, $df = 1, 140$, $p = 0.616$), but did vary among depths ($F = 7.78$, $df = 4, 140$, $p < 0.001$), and by year × depth interactions ($F = 6.48$, $df = 4, 140$, $p < 0.001$; Fig. 4). Algal

biomass corrected for rock area was lower at the deepest depth than the three shallowest depths.

Dreissena biomass encrusted on rocks fluctuated between 1995 and 1998 ($F = 38.23$, $df = 3, 329$, $p < 0.001$), among depths ($F = 30.75$, $df = 4, 329$, $p < 0.001$), and by year × depth interactions ($F = 3.40$, $df = 12, 329$, $p < 0.001$; Fig. 5). For example, Dreissena-encrusted rocks contained an average of 0.023 g/cm^2 of biomass at the shallowest depth, compared to 0.121 g/cm^2 at the deepest depth. Dreissena biomass corrected for rock area was lower in 1996 than 1995 and higher in 1997 and 1998 compared to 1996. Thus, the rank order of Dreissena biomass corrected for rock area is 1995, 1998, 1997 and 1996.

Mussel species composition on rocks changed slightly from 1996 to 1998. In 1996, 99.91 % of mussel-wet biomass was D. polymorpha, while in 1998 its biomass declined to 95.87 %. Wet and dry mussel mass including shells was highly correlated in 1997 (Pearson's $r = 0.998$) and 1998 (Pearson's $r = 0.999$).

Echinogammarus abundance

Year, depth and year × depth interactions were significant for Echinogammarus on Dreissena-encrusted rocks from 1995 through 1998 (MANOVA; Table 2). Echinogammarus abundance varied among years on Dreissena-encrusted rocks (Univariate test; Table 2). Its abundance was highest in 1995, lowest in 1996 and showed a general decrease through 1997 and 1998 (Fig. 6). For example, Echinogammarus abundance averaged 0.590 individuals/cm^2 1995, but only 0.176 individuals/cm^2 in 1998, a decrease of 70%.

Echinogammarus abundance was substantially lower on Cladophora- than on Dreissena-encrusted rocks in both 1997 and 1998 (Fig. 6). Across both years, there were approximately 80% fewer amphipods on rocks covered by this filamentous alga than on Dreissena-encrusted rocks.

Depth distributions of Echinogammarus on Dreissena-encrusted rocks varied from 1995 through 1998 (Fig. 7 a-d; Table 2). In 1995 and 1996, its lowest abundance occurred at the shallowest depth and its highest abundance at the central depth (Fig. 7 a,b). Abundance patterns at the deepest depths were intermediate to those at the shallowest and central depths. In 1997, its lowest abundance occurred at the shallowest depth on rocks encrusted with Dreissena, though it typically increased with increasing depth (Fig 7 c). Echinogammarus abundance remained relatively constant across all depths on Cladophora-encrusted rocks.

The 1998 abundance patterns were contrary to those from 1995 through 1997 on Dreissena-encrusted rocks. Echinogammarus had the highest abundance at the second depth (1.0 m) and its lowest abundance at the deepest depth (2.5 m) (Fig. 7 d). There was an increase in its abundance through the shallower depths and an overall decrease as depth increased. Abundance patterns on Cladophora-encrusted rocks were similar across all depths (Fig. 7 d).

Gammarus abundance

Year, depth and year × depth interactions were significant for Gammarus on Dreissena-encrusted rocks from 1995 through 1998 (MANOVA; Table 2). Gammarus

abundance varied among years on Dreissena-encrusted rocks (Univariate test; Table 2). Abundance increased significantly from 1995 to 1996, but fell to its lowest level in 1998 (Fig. 6). For example, Gammarus averaged 0.023 individuals/cm^2 in 1995 and 0.063 individuals/cm^2 in 1996, an increase of 175 %, but then decreased to only 0.005 individuals/cm^2 in 1998.

Gammarus abundance was similar on Cladophora- and on Dreissena- encrusted rock in both 1997 and 1998; however, its abundance was much lower than that of Echinogammarus on Cladophora-encrusted rocks (Fig. 6).

Depth distributions of Gammarus on Dreissena-encrusted rocks varied from 1995 through 1998 (Fig. 7 a-d; Table 2). In 1995 and 1997, its abundance was inversely related to lake depth (Fig. 7 a,c). By contrast, in 1996 its abundance remained relatively constant across all depths (Fig 7 b). In 1998, its abundance remained relatively low at all depths on Dreissena-encrusted rocks (Fig. 7 d).

Abundance patterns of Gammarus on Cladophora-encrusted rocks were similar across all depths and mirrored that of Dreissena-encrusted rocks for both 1997 and 1998 (Fig. 7 c,d).

The abundance of one amphipod species was weakly correlated with the abundance of the other species (Fig. 8). For example, when Gammarus abundance was at 0.34 Ind./cm^2, there were only 0.01 Echinogammarus/cm^2. Similarly, Echinogammarus abundance at 2.4 Ind./cm^2 yielded only 0.01 Ind./cm^2 of Gammarus. Moreover, the maximum number of Echinogammarus retrieved was 4.4 Ind./cm^2 from a 1995 sample, and no Gammarus were present on this Dreissena-encrusted rock.

1995 and 1996 amphipod interactions

The changes in amphipod abundance between 1995 and 1998 could potentially be attributable to differences in time of sample collection, and collection of specimens from different substrate types. Therefore, the years 1995-1996 and 1997-1998 were grouped together as sampling techniques and substrates gathered were comparable during each of these times. Amphipod abundances were subject to significant year and depth effects, but not to year × depth interaction effects on Dreissena-encrusted substrate from 1995 to 1996 (MANOVA; Table 3). Echinogammarus abundance varied between years and depths, but not by year × depth interactions (Univariate test; Table 3). Its abundance was higher in 1995 than in 1996, and was greatest at the central depths (Fig. 7 a,b).

Gammarus abundance, corrected for rock area varied between 1995 and 1996 and by depth, but did not demonstrate year × depth interaction effects (Univariate test; Table 3). Gammarus abundance was generally higher at shallower depths than at deeper ones (Fig. 7 a,b).

1997 and 1998 amphipod interactions

Abundances of both amphipod species were subject to significant year, depth, substrate, and year × depth interaction effects, but no substrate × depth interaction effects from 1997 to 1998 (MANOVA; Table 4). Echinogammarus abundance varied between year, depth, substrate, and year × depth interactions, but not by substrate × depth interactions (Univariate test; Table 4). Its abundance was higher in 1997 than in 1998, and was higher on Dreissena-encrusted rocks than on Cladophora-encrusted rocks (Fig. 7

c,d). Year × depth interactions were due to a shift in Echinogammarus abundance from deeper depths in 1997 to shallower depths in 1998.

Gammarus abundance varied by year, depth, and by a year × depth interaction, but not by substrate or a substrate × depth interaction effect (Univariate test; Table 4). Its abundance was higher in 1997 than in 1998, and at shallower depths relative to deeper ones (Fig. 7 c,d). A significant year × depth interaction was due to a shift in abundance distributions with depth. In 1997, Gammarus abundance decreased with increasing depth, while in 1998 abundances were similar at each depth.

Hyalella abundance

Hyalella was also detected in the samples, but its abundance remained very low (< 0.03 %) from 1995 through 1998. Abundance patterns did not vary between years, depths or among the substrates types.

Rock area and Biomass Effects on Amphipod Abundance

Dreissena biomass had significant positive effects on Echinogammarus abundance (Fig. 9; Table 5); however, Echinogammarus selected smaller Dreissena-encrusted rocks to larger ones (Fig. 10; Table 5). Cladophora biomass had no effect on Echinogammarus' abundance, but it selected larger Cladophora-encrusted rocks to smaller ones (Fig 11; Table 5).

Gammarus abundance was inversely related to Dreissena biomass (Fig 9; Table 6); however, it selected larger Dreissena-encrusted rocks to smaller ones (Fig. 10; Table 6).

Cladophora biomass had significant positive effects on Gammarus abundance (Fig 12; Table 6), but its abundance was not affected by area of Cladophora-encrusted rocks (Table 6).

Discussion

1994 Lake Erie Amphipod Survey

Samples collected from Middle Sister, East Sister and Pelee Islands during June 1994 revealed that Echinogammarus was present in western Lake Erie at least a year prior to its initial discovery in 1995 by Witt *et al.* (1997). It has been suggested by Dermott *et al.* (1998) that this amphipod was present in the western approaches of Lake Erie during 1994, and this study confirms that speculation. Furthermore, it demonstrates that its earliest record of occurrence was before July 1995 as reported by Dermott *et al.* (1998) off Gibraltar Island in Lake Erie. Body length sizes classes (Fig. 3) demonstrate that Echinogammarus was a fully reproducing population with different generations at the time of collection in 1994. Yemelianova (1994) reported that gammarid amphipods require time to acclimatize to new surroundings after the initial invasion before they can begin successful reproduction. Therefore, I postulate that Echinogammarus invaded Lake Erie no later than 1993, the year legislation was implemented that requires ships entering the Great Lakes to exchange freshwater ballast with highly saline water (United States Coast Guard 1993). Dahl *et al.* (1995) sampled two sites in western Lake Erie in 1993 and failed to detect the presence of Echinogammarus. However, sites in that study were not in close proximity to the possible inoculation area reported in this study.

Ten Ponar samples were taken in 1994 in the lower Detroit River (Trenton Channel) where Witt *et al.* (1997) located Echinogammarus beneath concrete slabs and under wrack, yet its presence was not detected in my samples. This suggests that the species' occurrence in the lower Detroit River in 1995 may have resulted from migration of animals from Lake Erie. This hypothesis is consistent with results from Jaźdźewski (1980), who reported Echinogammarus as a litophilous species that prefers large flowing rivers. Moreover, the rapid spread of Echinogammarus from the western basin of Lake Erie to the Detroit River is consistent with the species pattern of spread to the North and Baltic Seas from the Black Sea (Jaźdźewski 1980, Jaźdźewski and Konopacka 1993).

Middle Sister Island Amphipod Survey

My research indicates that the amphipod community in western Lake Erie has undergone immense changes since the introduction of Echinogammarus. Year, depth and substrate tend to influence abundance patterns of amphipods in this basin, though Echinogammarus was present and often abundant at many surveyed sites. This is the first comprehensive study to specifically examine Echinogammarus and Gammarus abundance patterns and potential interactions. Echinogammarus abundance was higher than Gammarus abundance across all years and substrates. Thus, shortly after the arrival of Echinogammarus into the Great Lakes, it has dominated and restructured the amphipod community. This may have implications on energy transfer efficiencies to higher trophic levels (Dermott *et al.* 1998).

Year had an effect on amphipod abundance. Echinogammarus abundance generally decreased from 1995 through 1998 (Fig. 6), while Gammarus abundance increased from

1995 to 1996, then decreased to reach its lowest level in 1998. Yearly changes in abundance may be due to normal population fluctuations or other biological processes. In 1995 and 1996 amphipods were collected in June, while in 1997 and 1998 they were collected in August. This may account for the decrease in abundance of Gammarus, which exhibit reduced abundance of large individuals during August (Clemens 1950). However, this would not account for the decrease in abundance of Echinogammarus, which typically peaks reproductively in August (Köhn and Waterstraat 1990, Konopacka and Jesionowska 1995).

Amphipod abundances were also affected by depth (Fig. 7). In both 1995 and 1996, Echinogammarus had its lowest abundance on Dreissena-encrusted rock at the shallowest depth, and its greatest abundance at the central depth (~ 2.0 m). This is consistent with Köhn and Waterstraat (1990), who reported that Echinogammarus preferred habitat between 0 and 2 meters in German lakes; however, Echinogammarus abundance increased with increasing depth during 1997 (Fig. 7 c), contrary to their findings. In 1998, it did not display any patterns associated with depth, as abundances were similar across all depths. The increase in abundance at deeper depths in 1997 may represent seasonal depth migrations of larger organisms. Echinogammarus abundance on Cladophora-encrusted rocks did not vary across depths, or between 1997 and 1998.

Gammarus abundance on Dreissena-encrusted rocks did not vary significantly among depths in 1995, 1996 or 1998, yet were generally higher at shallower depths than deeper ones. However, in 1996, Gammarus abundance increased over the two shallower depths and decreased throughout the deeper depths. This pattern is consistent with other research on the Great Lakes that demonstrated that Gammarus prefers habitats less than

2.0 m (Ricciardi *et al.* 1997) and up to 9.1 m in depth (Bially and MacIsaac 2000). Gammarus abundance did not fluctuate with depth on Cladophora-encrusted rocks in 1997 and 1998, and densities were similar to those on Dreissena-encrusted rocks.

Both amphipod species were present on Dreissena- and Cladophora-encrusted rocks; however, abundances displayed some differences on these substrates. Echinogammarus was more abundant on Dreissena-encrusted rocks than on Cladophora-encrusted rocks, whereas Gammarus abundance was similar on Cladophora- and Dreissena-encrusted rocks. Furthermore, abundance patterns of both species may be affected by the presence of heterospecifics. Competitive interactions may occur among amphipod species on the habitats as there was a weak negative trend of amphipod abundances (Fig. 8). For example, when Echinogammarus abundance was high (4.4 Ind./cm^2), Gammarus abundance was low, while the opposite pattern occurred when Gammarus abundance was high (0.34 Ind./cm^2).

Echinogammarus abundance was positively affected by Dreissena-encrusted biomass, while Gammarus abundance declined with increased Dreissena biomass. Biomass of Cladophora encrusted on rocks had no effect on Echinogammarus abundance, but it did have positive effects on Gammarus abundance.

Dreissena rock size had positive effects on Gammarus abundance, but Echinogammarus selected smaller Dreissena-encrusted rocks to larger ones. Gammarus abundance was not affected by Cladophora rock size, but Echinogammarus selected larger Cladophora rocks to smaller ones.

Echinogammarus abundance

Echinogammarus abundance was high among Dreissena-encrusted rocks during this study, a finding that supports work by other researchers and which suggest a close relationship between these species (Köhn and Waterstraat 1990, Pinkster 1993, Konopacka and Jesionowska 1995, Stewart *et al.* 1998a, González and Downing 1999, Burkart 1999, Stewart *et al.* 1999, Bially and MacIsaac 2000, Chapter 2, Chapter 3). For example, Dermott *et al.* (1998) reported over 18,000 Echinogammarus/m^2 on Dreissena-encrusted rocks at a depth of 5 m off Gibraltar Island in Lake Erie. Similarly, in this study Echinogammarus abundance was closely related to Dreissena biomass (Fig. 9). Echinogammarus could potentially benefit two ways living in amongst Dreissena. First, by hiding within Dreissena colonies the amphipods are less vulnerable to predation (González and Downing 1999, Burkart 1999, Stewart *et al.* 1999). Secondly, they may experience higher food concentrations in the Dreissena colonies (Köhn and Waterstraat 1990). For example, Burkart (1999) determined that feces and pseudofeces were able to sustain Echinogammarus living within Dreissena colonies.

Echinogammarus may preferentially exploit Dreissena habitat owing to long-term co-evolution of these species in Eurasia, which could serve to reduce predation risk (Köhn and Waterstraat 1990, Pinkster 1993, Konopacka and Jesionowska 1995). Thus, introduction and spread of Dreissena in the Great Lakes appears to have facilitated Echinogammarus' colonization, establishment and dispersal in a manner consistent with Simberloff and Von Holle's (1999) 'invasional meltdown' hypothesis.

Echinogammarus abundance exhibited a general decline on Dreissena-encrusted rocks from 1995 through 1998. Its highest abundance occurred in 1995, shortly after its

invasion. This pattern is consistent with observations of other researchers who report a rapid increase and then decline of exotic species following invasion (Elton 1958, Lodge 1993, Williamson and Fitter 1996). Echinogammarus' decrease in abundance on Dreissena-encrusted rock from 1995 to 1996 is most likely related to the reduction of Dreissena biomass adjusted for rock area, which occurred during 1996 (Fig. 5). However, Echinogammarus abundance continued to decrease in 1997 and 1998 even though area-adjusted Dreissena biomass equaled or surpassed 1995 values. This decline may be attributable to the presence of round nose goby (Neogobius melanostomus), which itself invaded and increased in abundance in western Lake Erie during this time (personal observation). Kuhns and Berg (1999) reported that presence of round goby in Lake Michigan decreased non-mussel invertebrate densities by 44%, and had an adverse effect on gammarid amphipod abundances. Other researchers in the Great Lakes have reported consumption of amphipods by gobies (Jude and Deboe 1996, Dubs and Corkum 1996). Moreover, Shorygin (1952) reported that gammarid amphipods comprise 34% by weight of juvenile round nose goby diet in its native range. Thus, the observed decrease in Echinogammarus abundance may be related to presence of predatory gobies. Other fishes may have accentuated this decline. For example, smallmouth bass (Micropterus dolomieui) and rock bass (Ambloplites rupestris) have been reported to reduce Echinogammarus abundance in high-Dreissena biomass treatments (Stewart *et al.* 1999).

I observed a significant positive relationship between Echinogammarus abundance and Cladophora rock area consistent with findings of Dick and Elwood (1996) who reported that the marine amphipod Echinogammarus marinus tended to select larger rocks (>250 mm) fouled by seaweed (Fucus spp.) over smaller ones.

Echinogammarus abundance decreased with increasing Dreissena rock size (Fig. 10). This finding is consistent to those of Dick and Elwood (1996), who demonstrated E. marinus preferred small stones and bare rocks (2-200 mm) to larger rocks. Although this correlation was statistically significant, the affinity was very low ($R^2 = 0.07$), and is possibly due to the large sample size (n = 346).

Gammarus abundance

Gammarus had similar abundances from 1995 through 1998 on Dreissena-encrusted rock. This finding is consistent with results from many other studies that have reported Gammarus among Dreissena colonies (Dusoge 1966, Dermott *et al.* 1993, Griffiths 1993, Bruner *et al.* 1994, Stewart and Haynes 1994, Wisenden and Bailey 1995, Botts *et al.* 1996, Ricciardi *et al.* 1997, Beckett *et al.* 1998, Stewart *et al.* 1998ab, Strayer *et al.* 1998, Burkart 1999, Bially and MacIsaac 2000, Chapter 2, Chapter 3). Gammarus, much like Echinogammarus, may utilize interstitial spaces between Dreissena shells as refuge from predators and abiotic stresses (Botts *et al.* 1996, Stewart *et al.* 1998ab). It may also benefit from production of feces and pseudofeces by Dreissena (Griffiths 1993, Dermott *et al.* 1993, Stewart and Haynes 1994, Wisenden and Bailey 1995, Botts *et al.* 1996, Ricciardi *et al.* 1997, Stewart *et al.* 1998ab, Kuhns and Berg 1999, Bially and MacIsaac 2000). The increase in Gammarus abundance from 1995 to 1996 may be related to the area of rocks collected and associated Dreissena-encrusted biomass. Rocks collected in 1996 were much larger than those collected in all other years and Gammarus abundance increased significantly on larger sized rocks (Fig. 10). The lowest recorded Dreissena biomass corrected for rock area among all the years was also observed in 1996, and

Gammarus abundance displayed an inverse relationship with Dreissena biomass (Fig. 9). Thus, the increase in Gammarus abundance in 1996 may be related to a combination of these two conditions.

Gammarus abundance was similar on Cladophora- and on Dreissena-encrusted rocks in 1997 and 1998, and it did respond positively to Cladophora biomass. This finding supports evidence from other studies that have noted Gammarus on rocks encrusted with Cladophora (Clemens 1950, Taft 1975, Delong *et al.* 1993, Stewart and Haynes 1994, Summers *et al.* 1997, Dermott *et al.* 1999).

Echinogammarus and Gammarus interactions

My research revealed that a high abundance of one amphipod species was correlated with a low abundance of the other, possibly reflecting weak interspecific competition (see Fig. 8). This finding is consistent with previous studies that have predicted (Witt *et al.* 1997) or demonstrated (Dermott *et al.* 1998, Burkart 1999) replacement of Gammarus by Echinogammarus. Moreover, Mordukhai-Boltovskoi (1958) noted displacement of native freshwater amphipods by Echinogammarus in the Caspian Lake. Both species were abundant on Dreissena-encrusted rocks, but Echinogammarus had a much stronger affinity for this substrate than did Gammarus. This outcome is also contrary to results from Chapter 2 that failed to detect any interaction between the amphipod species, and that of Chapter 3 that provided weak evidence for a positive relationship between densities of these amphipod species. Thus, the interaction between these two species of amphipod is neutral over short time periods (24 hours; Chapter 2), commensal over brief

time periods (72 hours; Chapter 3), and negative over longer periods of time (this study) due to amphipod abundances.

In summary, my research revealed that Echinogammarus ischnus was present in western Lake Erie in 1994, at least a year prior to its reported discovery. Moreover, based on size distributions of the 1994 population, it seems likely that some individuals were present in the lake as early as 1993. Echinogammarus abundance has decreased over time since its arrival, while Gammarus abundance remained relatively constant, but always significantly lower than Echinogammarus abundance. Strong patterns of Echinogammarus abundance existed on substrates encrusted with Dreissena, while Gammarus abundance was similar on Cladophora- and Dreissena-encrusted rocks. Echinogammarus abundance was highly correlated with Dreissena biomass, while Gammarus abundance was inversely related. Abundance of each amphipod species changed with depth. Gammarus responded positively to Cladophora-encrusted biomass, while Echinogammarus did not. There existed weak evidence of competition between amphipod species as the abundance of one species corresponded inversely with the abundance of the other. Finally, establishment and dispersal of Echinogammarus in the Great Lakes is likely the result of facilitation by Dreissena, a vivid example of 'invasional meltdown' (Simberloff and Von Holle 1999).

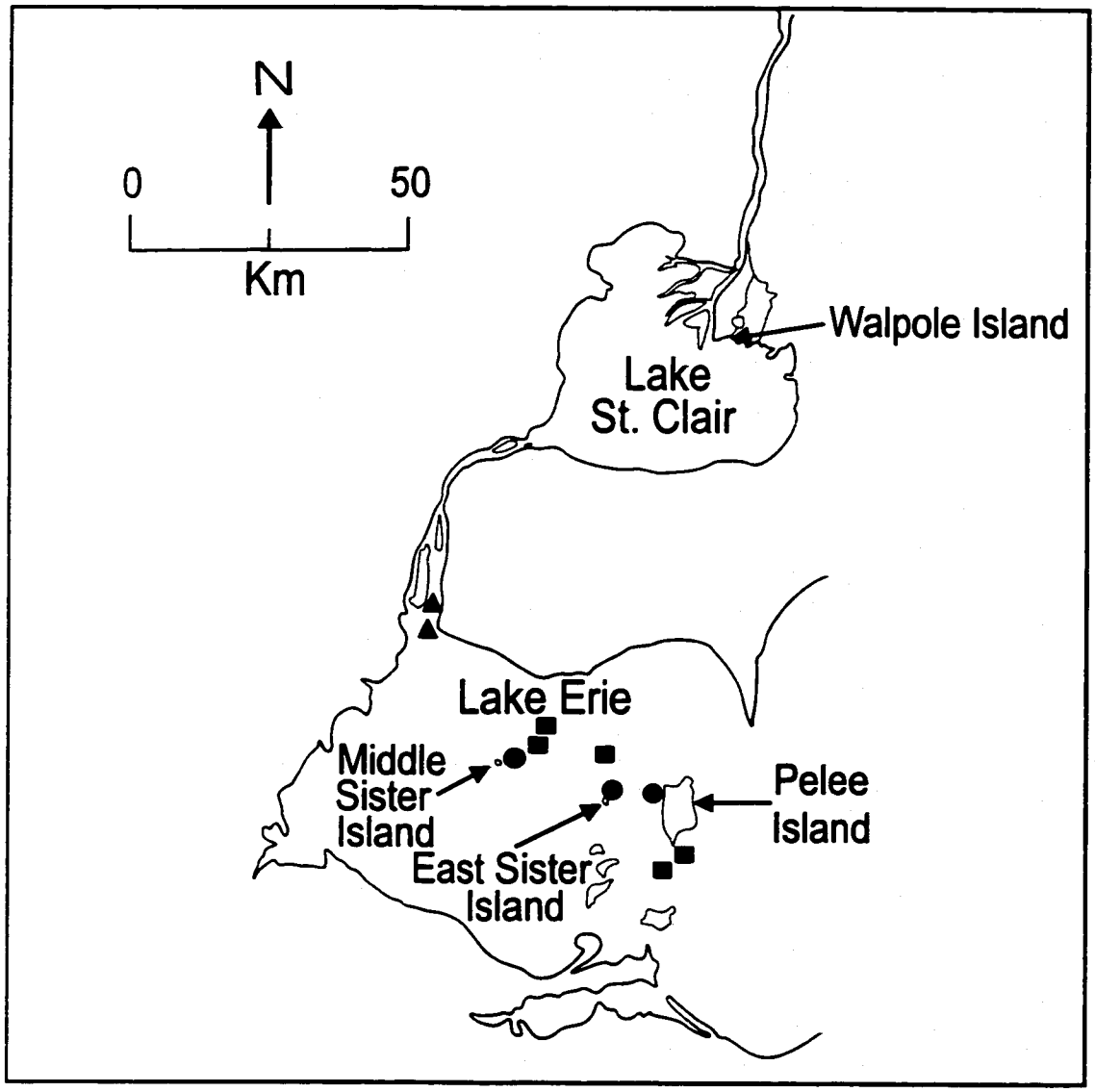


Figure 1. Location of sites sampled in western Lake Erie during 1994. Triangles represent sites where Gammarus fasciatus and Hyalella azteca were collected, squares where only G. fasciatus were collected, and circles where Echinogammarus ischnus and G. fasciatus were collected. Surveys were also conducted during 1995-1998 at Middle Sister Island, as was an amphipod colonization experiment during 1998. Animals for laboratory habitat preference experiments were collected during 1998 near Middle Sister and Walpole Islands.

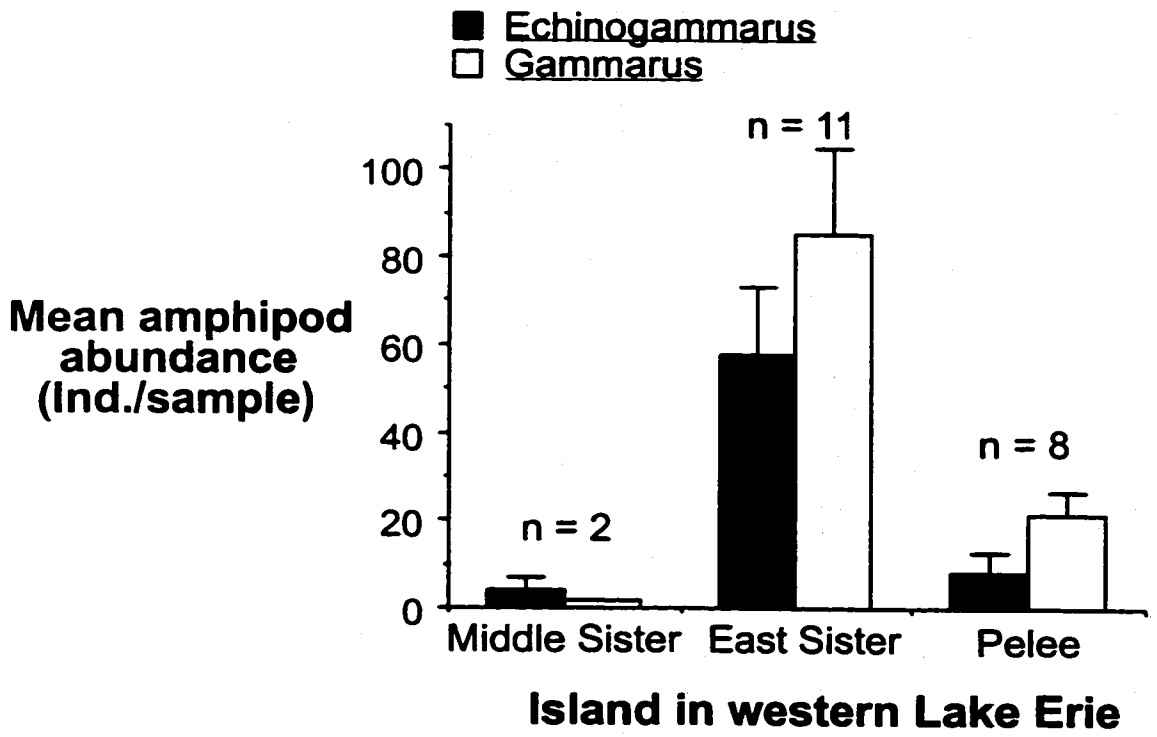


Figure 2. Mean abundance (± S.E.) of Echinogammarus ischnus and Gammarus fasciatus at three different islands in the western basin of Lake Erie from Ponar grab and rock samples collected in 1994.

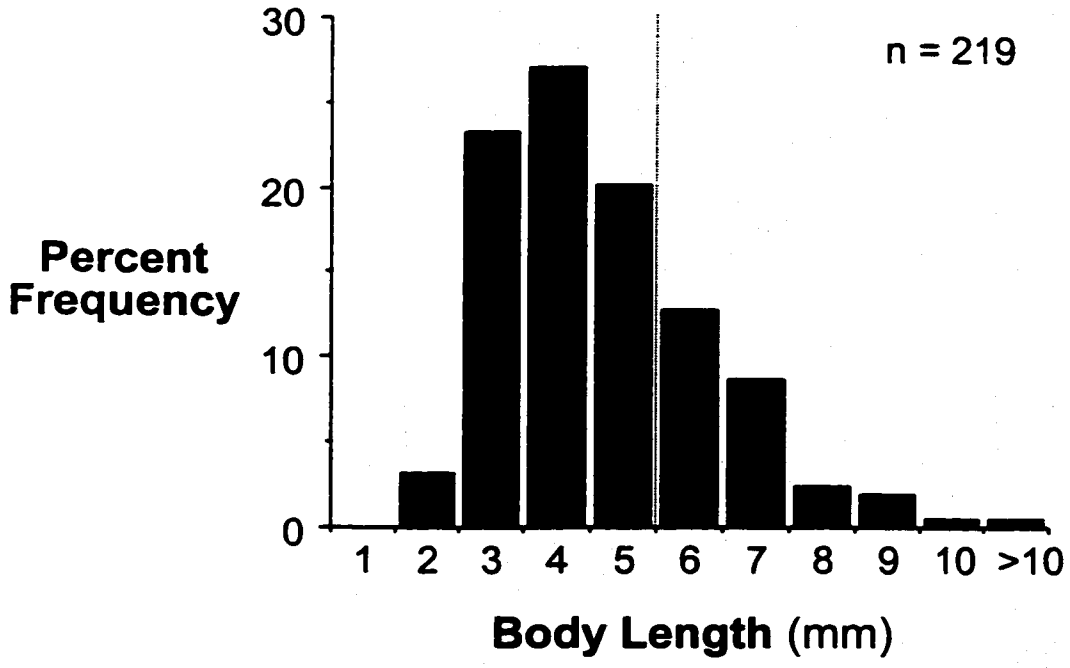


Figure 3. Body length size distributions of Echinogammarus ischnus from Ponar and rock samples collected at East Sister Island in western Lake Erie in 1994. Dotted line represents shift from juveniles to adults.

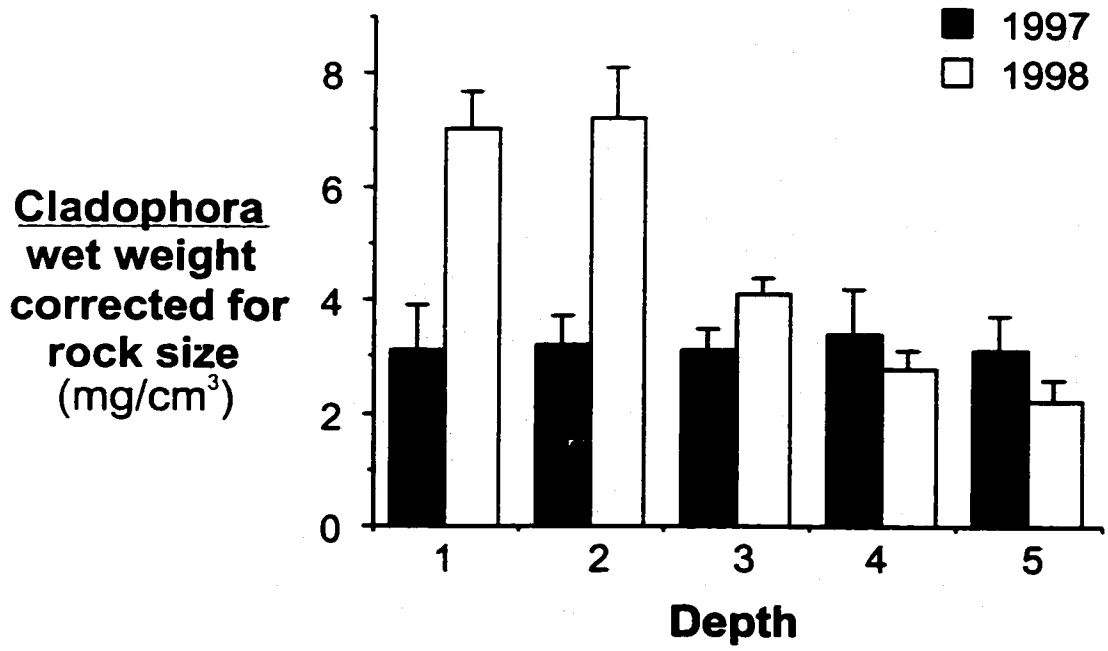


Figure 4. Cladophora glomerata wet weight (± S.E.) corrected for rock area (mg/cm^2) from Cladophora-encrusted rocks in 1997 and 1998. Depth is categorical with 1 being the shallowest and 5 the deepest.

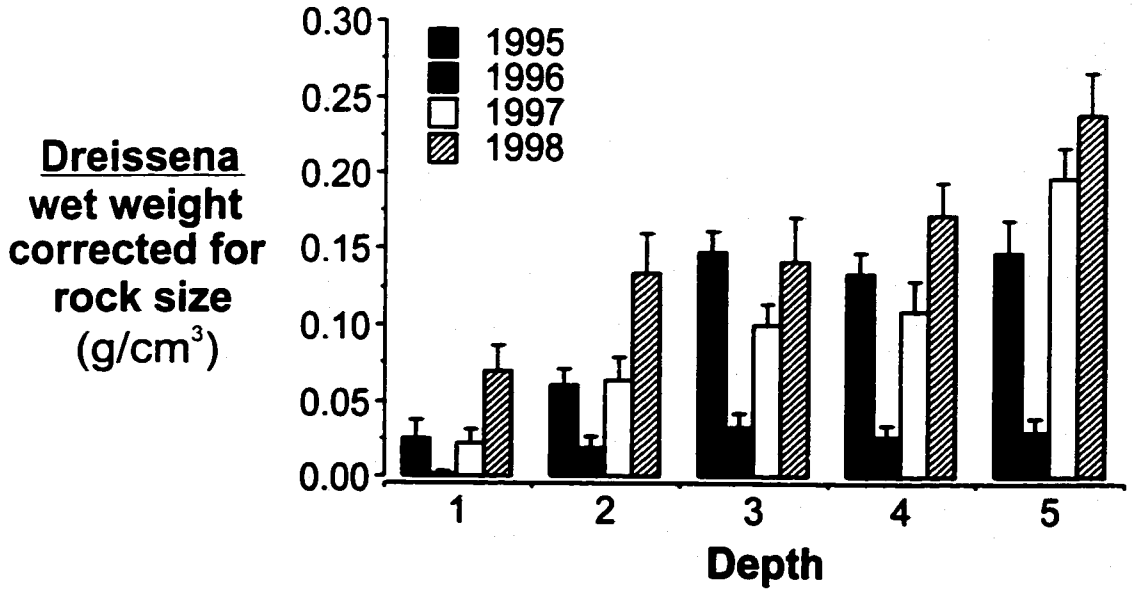


Figure 5. Dreissena spp. wet weight (± S.E.) corrected for rock area (g/cm^2) from Dreissena-encrusted rocks collected from 1995 through 1998. Depth is categorical with 1 being the shallowest and 5 the deepest.

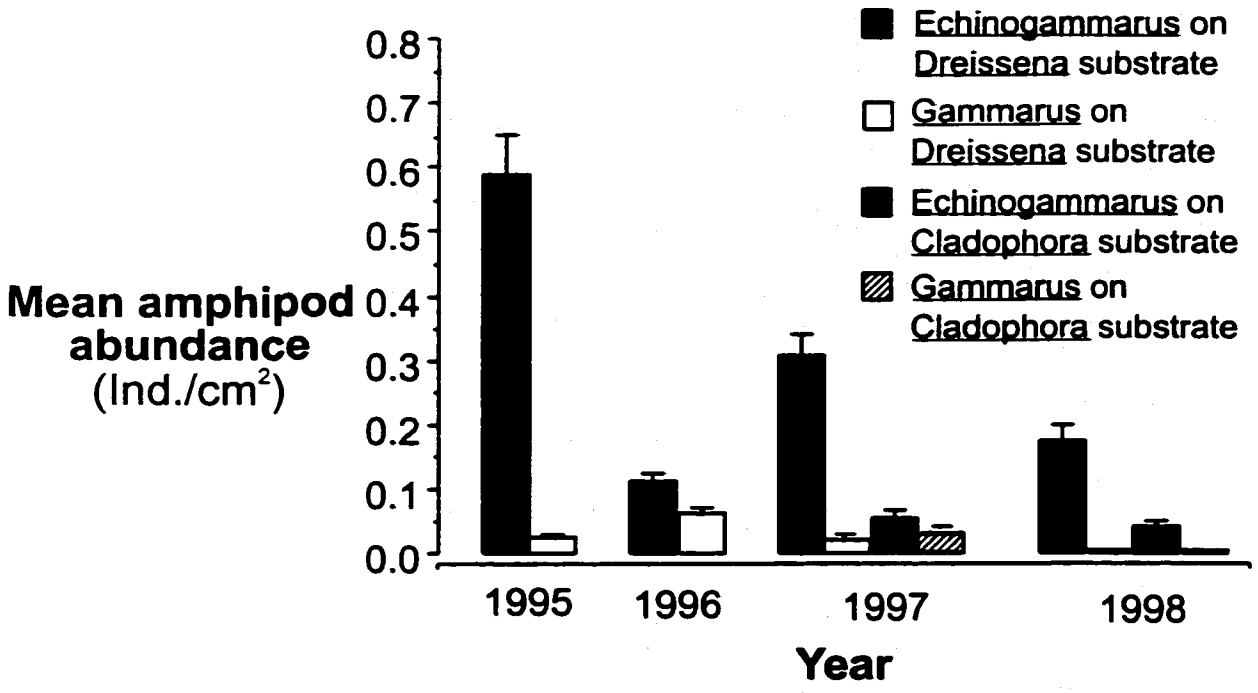
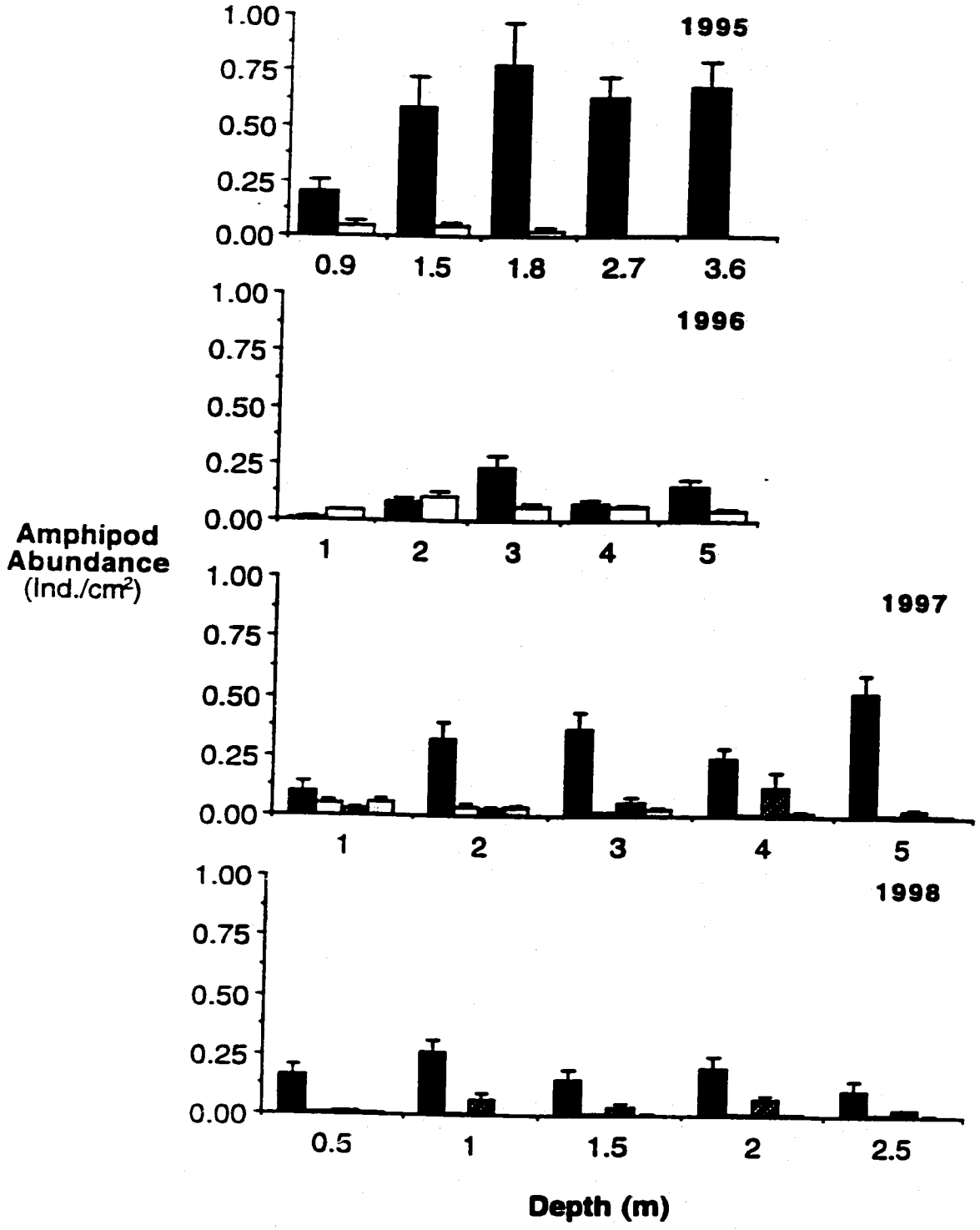


Figure 6. Mean abundance (± S.E.) of Echinogammarus ischnus and Gammarus fasciatus (Ind./cm²) on Cladophora- and Dreissena-encrusted substrate from 1995 through 1998.

Figure 7. Mean abundance (± S.E.) of Echinogammarus ischnus and Gammarus fasciatus (Ind./cm^2) on Cladophora- and Dreissena-encrusted substrate from 1995 through 1998 with depth. In 1995 and 1998, depth is measured in meters, and in 1996 and 1997, depth is categorical with 1 being the shallowest and 5 the deepest.


1995
1996
1997
1998
1.00
0.75
0.50
0.25
0.00
0.9
1.5
1.8
2.7
3.6
1
2
3
4
5
0.5
1
1.5
2
2.5
Amphipod Abundance (Ind./cm²)
Depth (m)

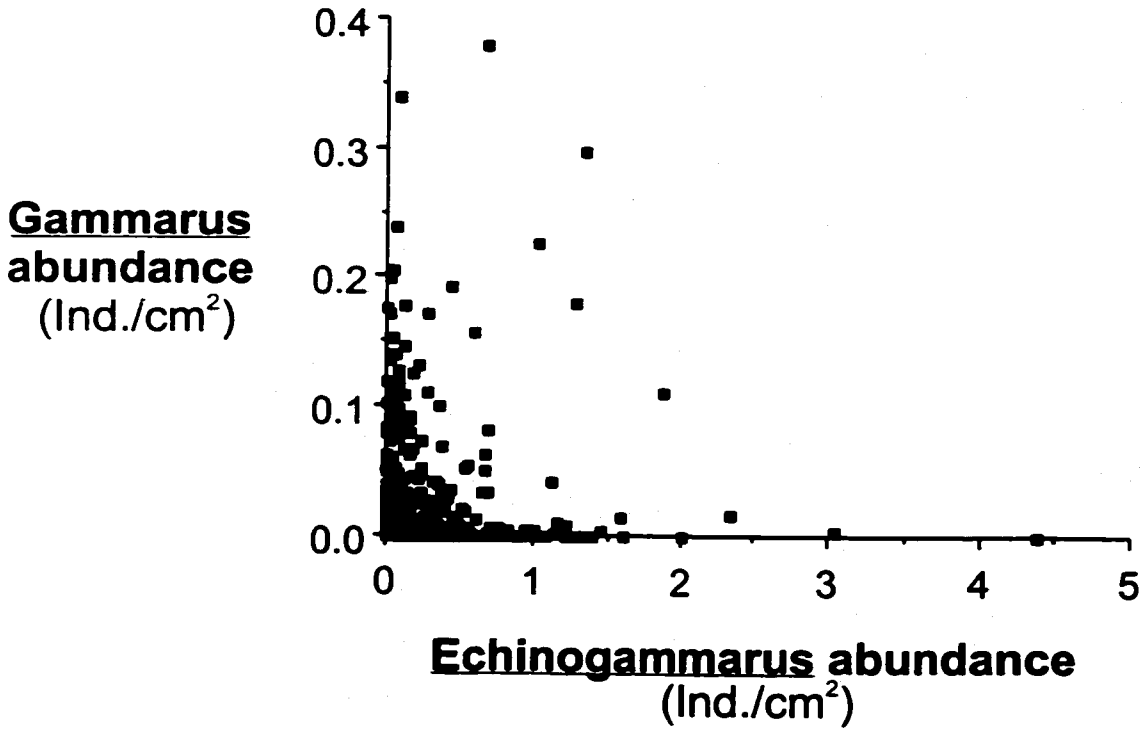


Figure 8. Relationship between Echinogammarus ischnus abundance (Ind./cm^2), and Gammarus fasciatus abundance (Ind./cm^2) from 1995 through 1998 on Cladophora- and Dreissena-encrusted rocks (n = 500).

Figure 9. Relationship between abundance of Echinogammarus ischnus (Ind./cm^2), and abundance of Gammarus fasciatus (Ind./cm^2) with total Dreissena wet weight (g/cm^2). Note difference in y-axis scales.

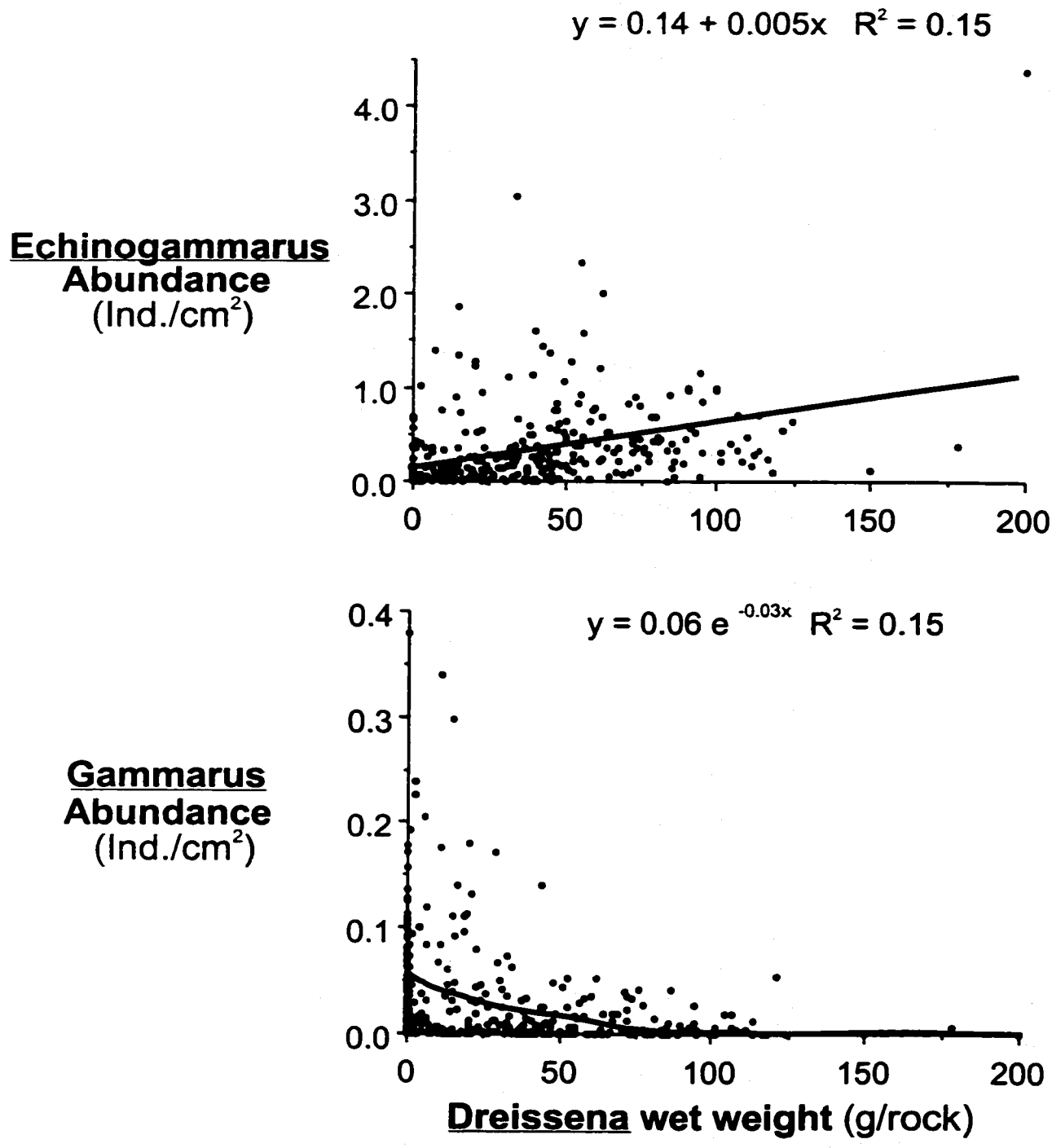
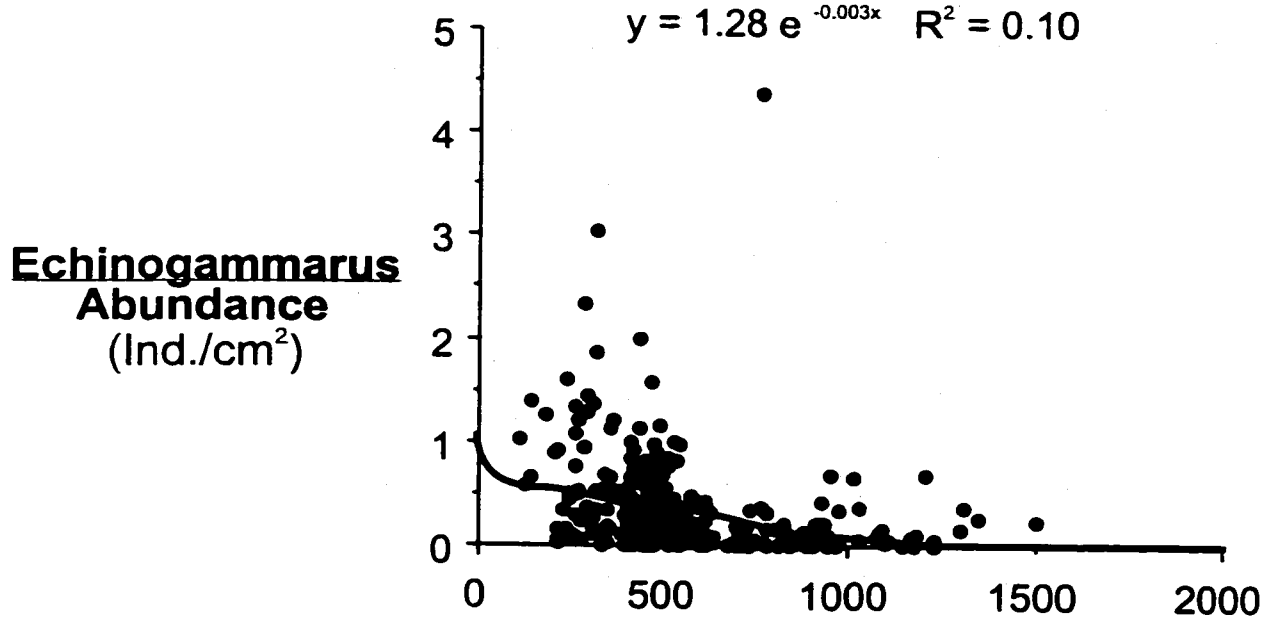
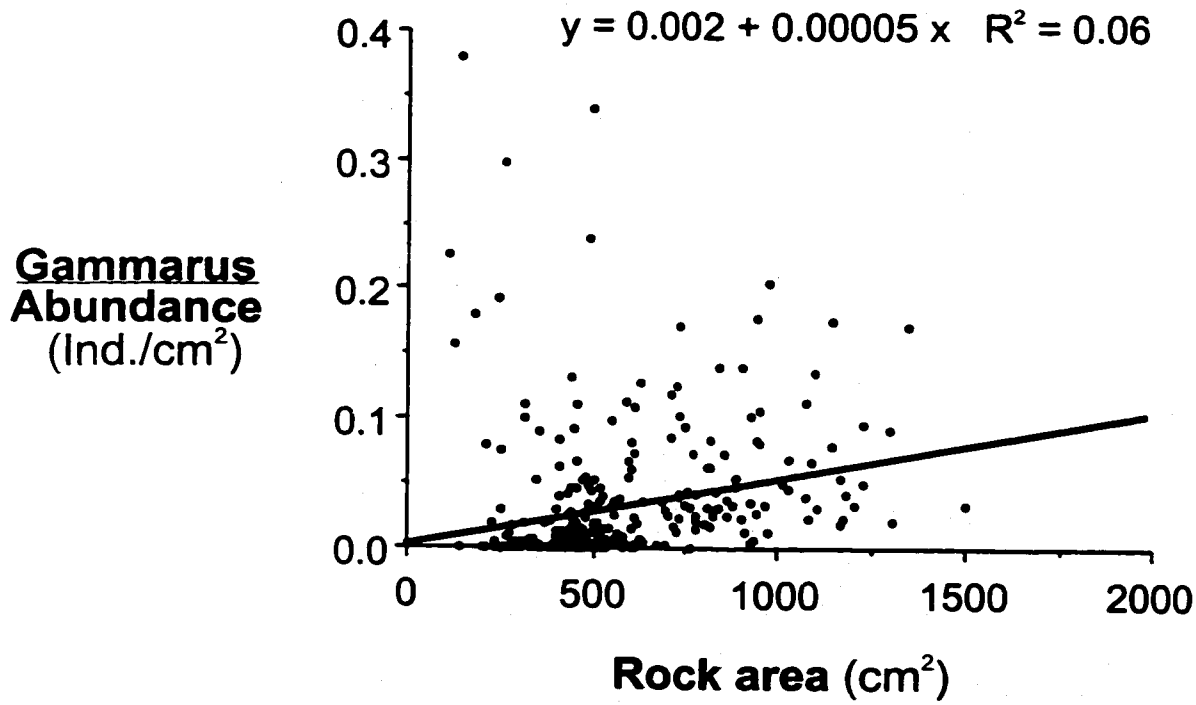

y = 0.14 + 0.005x R² = 0.15
Echinogammarus Abundance (Ind./cm²)
4.0
3.0
2.0
1.0
0.0
0
50
100
150
200
y = 0.06 e -0.03x R² = 0.15
Gammarus Abundance (Ind./cm²)
0.4
0.3
0.2
0.1
0.0
0
50
100
150
200
Dreissena wet weight (g/rock)

Figure 10. Relationship between abundance of Echinogammarus ischnus (Ind./cm^2) and rock area (cm^2), and abundance of Gammarus fasciatus (Ind./cm^2) and rock area (cm^2) on Dreissena-encrusted rocks. Note difference in y-axis scales.


y = 1.28 e -0.003x R² = 0.10
Echinogammarus Abundance (Ind./cm²)
5
4
3
2
1
0
0
500
1000
1500
2000


y = 0.002 + 0.00005 x R² = 0.06
Gammarus Abundance (Ind./cm²)
0.4
0.3
0.2
0.1
0.0
0
500
1000
1500
2000
Rock area (cm²)

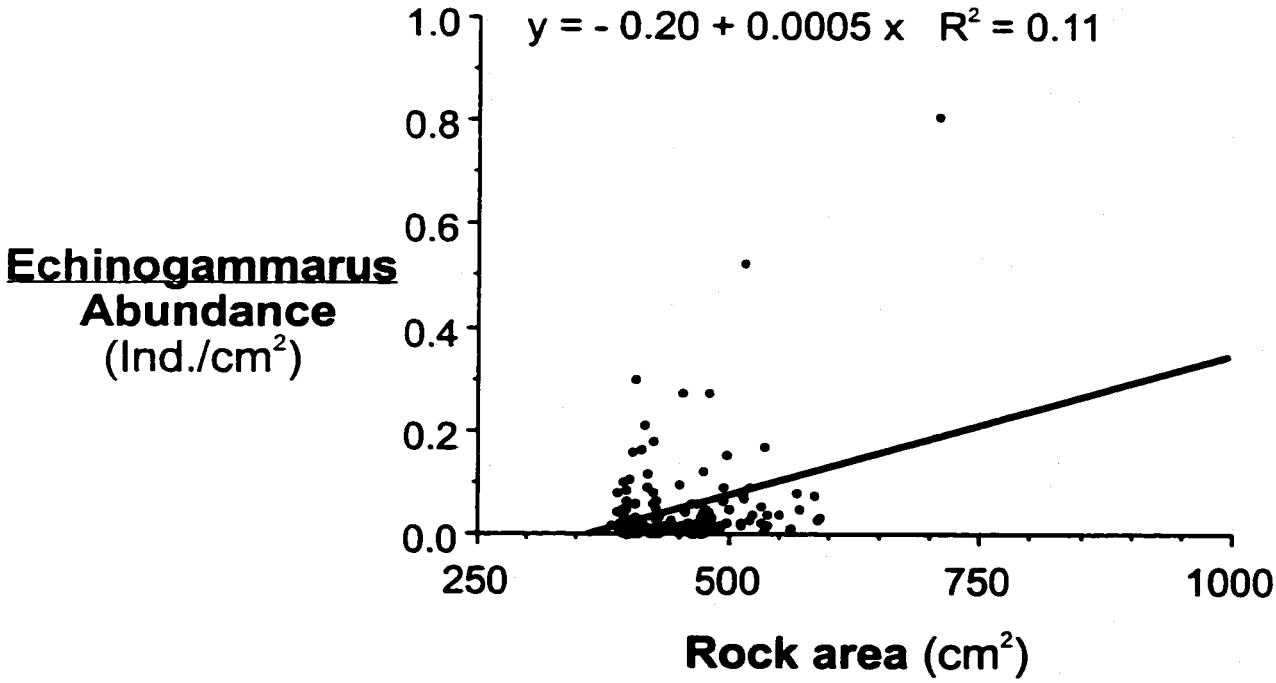


Figure 11. Relationship between abundance of E. ischnus (Ind./cm^2) and rock area (cm^2) on Cladophora-encrusted rocks.

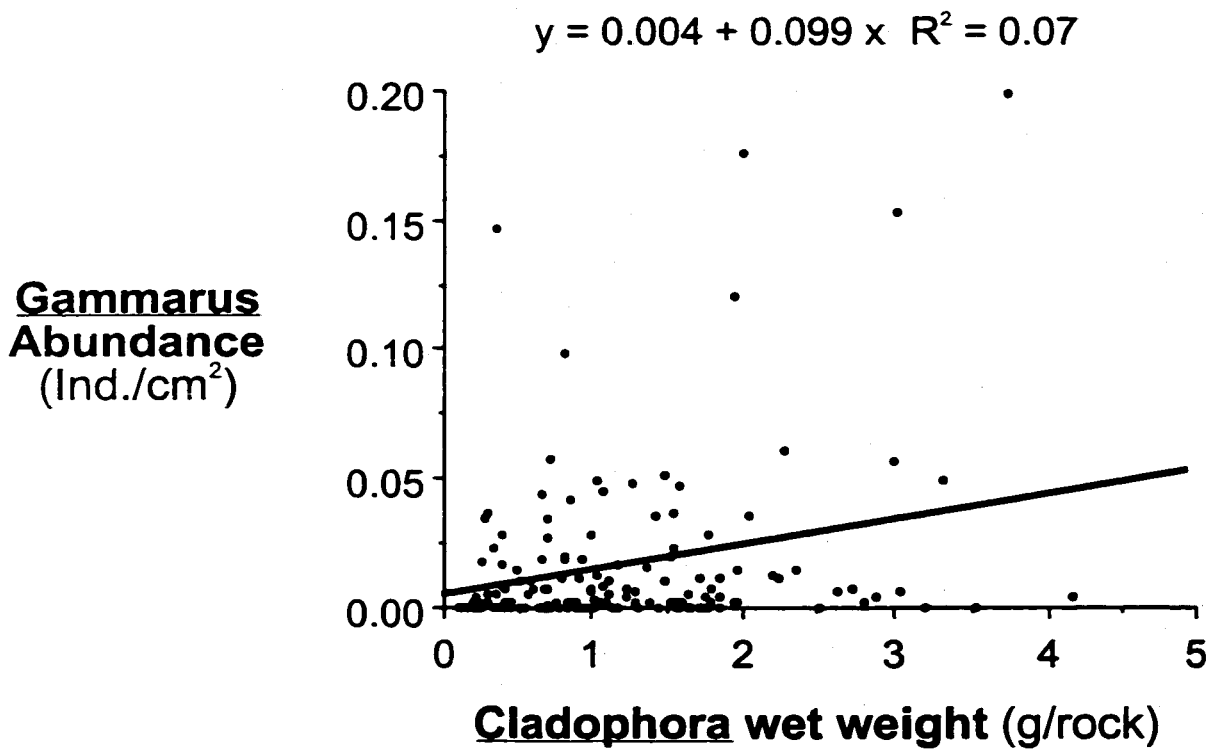


Figure 12. Relationship between abundance of G. fasciatus (Ind./cm^2) and Cladophora-encrusted biomass (g/rock).

Table 1. Review of sampling methods and techniques from 1995 through 1998.

Year	Methods
1995	• four transects; two each on west and east sides of island • five depths (0.9, 1.5, 1.8, 2.7, and 3.6 m) fixed • six Dreissena-encrusted rocks collected in June • rocks fixed in 5% Kahle's solution
1996	• three transects; one on west and two on east side of island • five depths fixed, but not recorded; categorical • six Dreissena-encrusted rocks collected in June • rocks fixed in 70% ethanol
1997	• three transects; one on west and two on east side of island • five depths fixed, but not standardized; categorical • five Cladophora- and 5 Dreissena-encrusted rocks collected in August • rocks fixed in 5% sugar-formalin solution
1998	• three transects; one on west and two on east side of island • five depths fixed and standardized (0.5, 1.0, 1.5, 2.0, and 2.5 m) • five Cladophora- and 5 Dreissena-encrusted rocks collected in August • rocks fixed in 5% sugar-formalin solution

Table 2. Two-way MANOVA on log X + 1 (amphipods/cm^2) from Dreissena-encrusted rocks from 1995 – 1998.

Test	Species	Independent variable	Wilk's Lambda	df	F-ratio	P
Multivariate		Year	0.574	6	35.05	< 0.001
		Depth	0.832	8	7.92	< 0.001
		Year × Depth	0.855	24	2.24	0.001
		Error		658		
Univariate	Echinogammarus	Year		3	38.02	< 0.001
		Depth		4	7.45	< 0.001
		Year × Depth		12	2.09	0.017
		Error		330		
	Gammarus	Year		3	30.60	< 0.001
		Depth		4	7.69	< 0.001
		Year × Depth		12	2.14	0.014
		Error		330		

Table 3. Multiple analysis of variance on abundances of Echinogammarus ischnus and Gammarus fasciatus (abundance divided by rock area and log X + 1 transformed) on Dreissena-encrusted rocks for the group 1995 to 1996.

Test	Species	Independent variable	Wilk's Lambda	df	F-ratio	P
Multivariate		Year	0.610	2, 189	60.39	<0.001
		Depth	0.786	8, 378	6.03	<0.001
		Year × Depth	0.931	8, 378	1.72	0.093
Univariate	Echinogammarus	Year		1	74.95	<0.001
		Depth		4	5.83	<0.001
		Year × Depth		4	1.10	0.358
		Error		190		
	Gammarus	Year		1	29.95	<0.001
		Depth		4	5.63	<0.001
		Year × Depth		4	1.93	0.107
		Error		190		

Table 4. Multiple analysis of variance on abundances of Echinogammarus ischnus and Gammarus fasciatus (abundance divided by rock area and log X + 1 transformed) on Dreissena-encrusted rocks for the group 1997 to 1998.

Test	Species	Independent variable	Wilk's Lambda	df	F-ratio	P
Multivariate		Year	0.804	2, 284	34.61	< 0.001
		Depth	0.832	8, 568	6.84	< 0.001
		Substrate	0.713	2, 284	57.18	< 0.001
		Substrate × Depth	0.956	8, 568	1.63	0113
		Year × Depth	0.840	8, 568	6.48	< 0.001
Univariate	Echinogammarus	Year		1	13.30	< 0.001
		Depth		4	3.54	0.008
		Substrate		1	114.64	< 0.001
		Substrate × Depth		4	2.65	0.034
		Year × Depth		4	4.50	0.002
		Error		285		
	Gammarus	Year		1	13.30	< 0.001
		Depth		4	10.98	< 0.001
		Substrate		1	0.59	0.444
		Substrate × Depth		4	0.59	0.673
		Year × Depth		4	9.25	< 0.001
		Error		285		

Table 5. Multiple regression analyses on abundance of Echinogammarus ischnus examining effects of rock area and Dreissena-encrusted biomass (1995-1998), and rock area and Cladophora-encrusted biomass (1997-1998). Rock area and encrusted biomass are independent continuous variables. (Dreissena and Cladophora biomass was corrected for rock area prior to analysis).

Substrate	Independent variable	df	F-ratio	P
Dreissena-encrusted rock	Rock area Dreissena biomass	2, 346	62.90	< 0.001
Cladophora-encrusted rock	Rock area Cladophora biomass	1, 147	9.54	< 0.001

Table 6. Multiple regression analyses on abundance of Gammarus fasciatus examining effects of rock area and Dreissena-encrusted biomass (1995-1998), and rock area and Cladophora-encrusted biomass (1997-1998). Rock area and encrusted biomass are independent continuous variables. (Dreissena and Cladophora biomass was corrected for rock area prior to analysis).

Substrate	Independent variable	df	F-ratio	P
Dreissena-encrusted rock	Rock area Dreissena biomass	2, 346	31.70	<0.001
Cladophora-encrusted rock	Rock area Cladophora biomass	1, 147	5.44	0.005

Laboratory experiment of habitat preference

Introduction

The Laurentian Great Lakes have been invaded by exotic species since the first settlement of Europeans. Exotic species numbers have increased linearly since the mid-1800's mainly due to the release of solid and liquid ballast (Mills *et al.* 1993). Since 1985, 70% of the exotic species that have established in the Great Lakes are native to the Ponto-Caspian region (the Black Sea, Azov Sea, and Caspian Lake) (Ricciardi and MacIsaac 2000). These species include fish (Neogobius melanostomus, Proterorhinus marmoratus, Gymnocephalus cernuus), and mussels (Dreissena polymorpha, D. bugensis). A recent invader from this region is the cladoceran Cercopagis pengoi, which was discovered in Lake Ontario in 1998 (MacIsaac *et al.* 1999). The most recent introduction reported is by the diatom Thalassiosira baltica in Lake Ontario (Edlund *et al.* 2000).

Ponto-Caspian amphipods (Class Crustacea) have also been discovered in the Great Lakes. For example, Echinogammarus ischnus was found in the lower Detroit River during 1995 (Witt *et al.* 1997), while Corophium mucronatum was detected in Lake St. Clair during 1997 (Grigorovich and MacIsaac 1999), though the latter has not established.

The amphipod, Gammarus fasciatus is of vital importance to aquatic food webs due to its consumption by crayfish Orconectes rusticus, yellow perch Perca flavescens, rock bass Ambloplites rupestris, and smallmouth bass Micropterus dolomieui (Stewart and Haynes 1994, Botts *et al.* 1996, Ricciardi *et al.* 1997, Stewart *et al.* 1998ab).

The invasion of Dreissena had a marked effect on the abundance and biomass of benthic organisms, and G. fasciatus appears to have benefited tremendously by Dreissena invasion. For example, Griffiths (1993) found that G. fasciatus increased from 80 to 400

Ind./m^2 on the north shore and from 520 to 3,580 Ind./m^2 on the south shore of Lake St. Clair. Similarly, Stewart *et al.* (1994) found this amphipod increased from 233 to 1,670 Ind./m^2 in Lake Ontario, while Dermott *et al.* (1993) reported that it increased from 1,146 to 24,114 Ind./m^2 in Lake Erie following Dreissena invasion. G. fasciatus lives in interstitial spaces between Dreissena shells, where it is afforded refuge from predators and abiotic disturbances (Botts *et al.* 1996, Stewart *et al.* 1998ab, Bially and MacIsaac 2000). To a lesser extent, the production of feces, pseudofeces and accumulating organic matter by Dreissena provides amphipods with a food source (Griffiths 1993, Dermott *et al.* 1993, Stewart and Haynes 1994, Wisenden and Bailey 1995, Botts *et al.* 1996, Ricciardi *et al.* 1997, Stewart *et al.* 1998ab).

The recent spread of Echinogammarus to Lake Huron and the St. Lawrence River from the Detroit River likely occurred by vagile and pagile dispersal and through anthropogenic means (Dermott *et al.* 1998). The widespread occurrence of Dreissena in the Great Lakes may have facilitated its rapid dispersal. Köhn and Waterstraat (1990) observed that Echinogammarus is closely associated with D. polymorpha in German lakes. Sites surveyed by Dermott *et al.* (1998) in the lower Great Lakes included sand, bedrock, gravel, cobble, Vallisneria, Cladophora and Dreissena substrates. Echinogammarus occurred at different densities in each of these habitats, but was most abundant in cobble substrates (Dermott *et al.* 1998).

Dispersal and population growth of Echinogammarus could potentially affect abundance of resident amphipods in the Great Lakes. For example, growth of Echinogammarus has been postulated to adversely affect abundance of Gammarus in Lake Erie (Dermott *et al.* 1998, González and Downing 1999).

It has been suggested by several researchers that replacement of amphipod species could have drastic implications for energy pathways in the Great Lakes due to Gammarus' vital importance in these foodwebs (Stewart and Haynes 1994, Botts *et al.* 1996, Ricciardi *et al.* 1997, Stewart *et al.* 1998ab). However, no mechanistic studies have been conducted in the laboratory or field to assess habitat preference by invading Echinogammarus, or its effects on resident Gammarus populations.

In this study, I examine habitat preferences of E. ischnus and G. fasciatus, as well as possible competitive interactions between the species on substrates of varying complexity. Specific hypotheses tested in this chapter are that:

1) amphipod habitat preferences are not affected by substrate complexity;
2) habitat preference is not affected by the presence of a potentially competing amphipod species or by amphipod density;

3) rock size and associated Cladophora or Dreissena biomass has no effect on amphipod habitat preferences.

Materials and Methods

I conducted a replicated lab experiment at the Great Lakes Institute for Environmental Research Centre to determine amphipod habitat preference. The experiment was conducted over a 24-hour period from July 17-18, and from August 13-14, 1998 in aquaria contained within an environmentally controlled chamber at 21° C and constant light. Forty-liter aquaria were filled with 20 L of filtered Detroit River water

(Watergroup sand filter, model # AMG-FDTX) and were aerated with stones in the center of the tank.

Collection of Organisms

Study organisms were collected from western Lake Erie at Middle Sister Island (see Fig. 1; Chapter 1), a small dolomite outcrop approximately 15.7 km from the Canadian mainland (for more information see MacIsaac 1996b), approximately 72 hours before experimentation. Rocks encrusted with either Cladophora or Dreissena spp. were collected at random from 0.5 and 2.0 m depths respectively, by use of snorkel or SCUBA, and placed into polypropylene bags (large Ziploc® freezer bags) which were sealed underwater and brought to the surface. Rocks were subjected to agitation in a bucket containing Lake Erie water for approximately one minute to dislodge amphipods, following which the rocks were returned to the lake bottom. Contents from the bucket were passed through a 1.0-mm sieve to capture large amphipods (while allowing juveniles to escape), and placed in a cooler containing Lake Erie water for transport to the laboratory. Using descriptions from Witt *et al.* (1997), E. ischnus and G. fasciatus were identified and sorted under a dissecting microscope (Zeiss Jena model Technival 2) at 5 X magnification, and placed into aerated 40 L aquaria (one for each amphipod species) containing 20L of filtered Detroit River water with Elodea canadensis as a food source.

Owing to the low abundance of G. fasciatus at the collection site, numbers were augmented by collections made in the Lake St. Clair river delta near Walpole Island (Fig. 1; Chapter 1) *via* repeated 100 m hauls of a benthic sled dredge (Wildco 171-D20) approximately 48 hours before experimentation. Collected amphipods were passed

through a 1.0-mm sieve, identified and separated under a dissecting microscope, and placed into their respective holding aquaria.

Experimental Design

Three equally sized substrate types were placed in each aquarium: i) bare rocks that were collected from Middle Sister Island from a previous study (MacIsaac 1996b), ii) Cladophora-encrusted rocks, and iii) Dreissena spp.-encrusted rocks. The latter two-substrate types were present on rocks collected from Middle Sister Island approximately 24 hours before the experiment. Rocks were agitated in a bucket of Lake Erie water for 5 minutes to remove all existing fauna, and allowed to acclimate in aquaria for 24 hours along with the bare rock. Rocks with all three substrate types were randomly arranged within each aquarium. A block of four study treatments, replicated five times, included: i) 50 Echinogammarus; ii) 50 Gammarus; iii) 25 Echinogammarus and 25 Gammarus (low density); and iv) 50 Echinogammarus and 50 Gammarus (high density) (Figure 1). These treatments were designed to assess amphipod habitat preferences, interspecific interactions, and total amphipod density effects.

Mature amphipods of varying size and sex were randomly selected from holding tanks, counted under a dissecting microscope, and placed into 1-L mason jars filled with filtered Detroit River water (Watergroup sand filter). Only healthy amphipods were used for the four treatments. After all amphipods were separated and placed into mason jars, one block of each of the four treatments was initiated by decanting contents of the mason jars into pre-marked aquaria (see Figure 1). All blocks were set up in the same manner. Aquaria walls were shrouded by paper to prevent human disturbance during the

experiment and reclamation procedure. After 24-hours, plastic dividers with silicone gaskets on their base were inserted into each aquarium to separate the rocky substrates. Dividers prevented amphipods from moving between substrates during the interval when animals were collected and preserved. All amphipods were associated with a substrate at the termination of each experiment (i.e. none were located in the open water or at the aquarium surface). Rocks were removed one at a time from each aquarium, rinsed with filtered Detroit River water, and the amphipods collected into a 40-μm-mesh sieve. Animals were placed into vials and fixed in 5% sugar-formalin. Amphipods that detached from a substrate while being removed were captured with a net and fixed. After all rocky substrates were removed from the tanks, fixed amphipods were identified and counted under a dissecting microscope, with the substrate upon which they settled recorded. Dreissena- and Cladophora-encrusted rocks were scraped clean with a surgical blade and material stored in 500-mL mason jars with 5% sugar-formalin.

Analysis of rock area and associated biomass

Volume of experimental rocks was measured by water displacement. Three measures of volume were made for each rock and the mean calculated. Volume of rocks was then converted to area (cm^2) from surface area-rock volume correlations calculated by MacIsaac (1996b).

Dreissena samples were cleaned by removing broken shells and byssal threads, separated by species and blotted dry. Wet mass of each species was assessed using an AND FX-200 electronic balance. Right valve lengths of all mussels from the samples were measured to the nearest 0.1-mm using Manostat vernier calipers (model # 15-100-500). D. polymorpha and D. bugensis dry weights were determined by placing measured

mussels on pre-weighed dried aluminum boats (60° C, 24 hours) in an oven for 48 hours at 60° C. Cladophora wet weight was determined on the electronic balance after samples were compressed between paper towels to remove excess water.

Statistical Analysis

Variation in rock area was assessed using analysis of variance with treatment, habitat, and date entered as categories. A habitat × date interaction effect was also included in the analysis. To determine whether substrate biomass varied across treatments or between dates, separate 2-way ANOVA's were conducted for each Cladophora and Dreissena using treatment and date as independent variables. Dreissena or Cladophora wet weight biomass was divided by rock area prior to analysis. A separate 2-way ANOVA was also conducted on average mussel size of Dreissena-encrusted on rocks with treatment and date as independent variables.

The number of amphipods retrieved from the three substrates in each aquarium was summed and the proportion on each substrate determined. Some amphipods were lost, possibly due to the reclamation technique or to cannibalism (Dediu 1980). In these cases, the retrieved amphipod number was utilized to calculate proportions. Proportions of animals using each substrate in each aquarium were arcsine (square root) transformed before analysis in Systat (Version 8.0).

Separate general linear models (4-way ANOVA) were used to determine habitat preferences of, and interspecific interactions between, amphipod species. The arcsine square root proportional abundance of an amphipod species was entered as the dependent

variable while habitat, date, treatment and block were independent categorical variables. Interaction effects examined included habitat × date and treatment × habitat. If significant differences were found, Bonferroni multiple comparison tests (at $\alpha = 0.05$) were utilized to explore the nature of the differences.

Analysis of covariance (ANCOVA) tests was used to determine the effect of rock area on habitat preference. The transformed proportional abundance of the amphipod species was entered as the dependent variable, habitat and treatment as categorical independent variables, and with rock area entered as the covariate. Habitat × rock area, and treatment × rock area interaction effects were also included in the model. Separate analyses were conducted for Echinogammarus and Gammarus.

To determine effects of rock area, biomass encrusted on experimental rocks, and mean mussel size on amphipod habitat preference, separate multiple linear regressions were conducted. The transformed proportional abundance of each amphipod species was entered as the dependent variable and either rock area of each substrate type, or Cladophora and Dreissena total wet weight biomass, or mean mussel size encrusted on rocks were entered as independent continuous variables.

Results

Substrates

Rock area did not differ between the four treatments ($F = 0.78$, $df = 3, 111$, $p = 0.506$), among the three substrates ($F = 1.24$, $df = 2, 111$, $p = 0.293$), or between substrate

× date interactions ($F = 2.03$, $df = 2, 111$, $p = 0.136$). However, rocks were significantly smaller in the second set of experiments ($F = 102.87$, $df = 1, 111$, $p < 0.001$).

Cladophora-encrusted biomass on the rocks did not vary among any of the treatments ($F = 0.94$, $df = 3, 35$, $p = 0.430$). However, Cladophora-encrusted biomass was significantly lower in August than in the July experiment ($F = 39.63$, $df = 1, 35$, $p < 0.001$). For example, rocks contained an average of 6 mg/cm^2 of Cladophora during July, but only 1 mg/cm^2 during August (Table 1).

Dreissena-encrusted biomass did not differ between the treatments ($F = 1.50$, $df = 3, 34$, $p = 0.233$), however it did differ between experimental dates ($F = 26.15$, $df = 1, 34$, $p < 0.001$; Table 1). Average mussel size on Dreissena substrate did not differ between the treatments ($F = 2.87$, $df = 3, 35$, $p = 0.050$; Table 1), but were larger in August than in July ($F = 6.35$, $df = 1, 35$, $p = 0.016$; Bonferroni's test). Relative abundance on Dreissena-encrusted rocks was 97 % D. polymorpha and 3 % D. bugensis (wet weight). Wet and dry mussel mass were highly correlated (Pearson's $r = 0.996$).

Echinogammarus habitat preference

Echinogammarus had highly significant habitat preferences in isolation and when present with Gammarus in both low- and high-density treatments (Table 2; Fig. 2). Dreissena- substrate was preferred to Cladophora-encrusted substrate and both were preferred over bare substrate (Bonferroni's test). Habitat preference did not vary by amphipod treatment, experimental date, or experimental blocks (Table 2; see Fig. 1). However, there were significant habitat × date interaction effects (Table 2). For example, while Dreissena- rocks were significantly preferred over both Cladophora- and bare rocks

in both experiments, Cladophora-encrusted rocks were only preferred over bare rocks in the July experiment (Bonferroni's test). Cladophora-encrusted and bare substrates were selected equally in the August experiment (Fig. 3). Habitat × block interaction effects also occurred in August, as Echinogammarus selected Dreissena-encrusted and bare substrate equally in one of the blocks.

Gammarus habitat preference

Gammarus also had strong habitat preferences in isolation and in the presence of Echinogammarus (Table 3; Fig. 4). Cladophora- and Dreissena-encrusted substrates were both preferred over bare substrate, but were themselves selected equally (Bonferroni's test). Habitat preference did not change when Echinogammarus was present in either low- or high-density treatments. No significant effects were observed between experimental dates, experimental blocks, or by substrate × treatment interactions (Table 3). However, like Echinogammarus, there were significant habitat × date interactions (Table 3). Dreissena was negatively selected over Cladophora in the July experiment, while in August the two substrates were selected equally (Figure 5).

Amphipod habitat use and rock area

Echinogammarus abundance did not change significantly with habitat, treatment, rock area, habitat × rock area, or treatment × rock area interaction effects (ANCOVA; Table 4). Echinogammarus had no preference for smaller bare rocks to larger ones (Table 5). Neither size of Cladophora-encrusted rocks, nor encrusted Cladophora biomass had any

effect on habitat partitioning (Table 5). Echinogammarus did not select smaller Dreissena- rocks to larger ones, and had no significant relationships with total Dreissena-encrusted biomass (Table 5). Mean size of mussels encrusted on rocks had no effect on Echinogammarus habitat partitioning (Table 5).

Gammarus was not significantly affected by habitat, treatment, rock area, habitat × rock area, or treatment × rock area interaction effects (ANCOVA; Table 6). Gammarus did not select smaller bare rocks to larger ones (Table 7). Size of Cladophora- and Dreissena-encrusted rocks had no effect on habitat partitioning (Table 7). Moreover, total Cladophora- and Dreissena-encrusted biomass had no effect on Gammarus habitat partitioning (Table 7). Mean size of mussels encrusted on rocks had no effect on habitat partitioning (Table 7).

Discussion

This is the first study to examine Echinogammarus and Gammarus habitat preferences in single and mixed species experiments in the laboratory. González and Downing (1999) studied amphipod habitat preferences in field settings, however, they did not differentiate habitat preferences of each species separately, but reported a combined response. They also detected that amphipods preferred highly complex substrates to bare rocks only in late summer (August). This study found that both amphipod species preferred highly complex substrates to bare rock in both July and August.

My experimental tests illustrated definitive habitat preferences for each species of amphipod. Both amphipod species preferred substrates with a higher degree of

complexity to bare substrate. However, the two species exhibited some differences with respect to their selection of Dreissena- and Cladophora-encrusted rocks. Echinogammarus preferred Dreissena to Cladophora habitat very strongly, while Gammarus preferred the two complex substrates equally. Habitat preferences of both species were unaffected by amphipod density, and by the presence of heterospecific amphipod species. Thus, while the species illustrated habitat preferences, these selections were not influenced by the presence of heterospecific individuals or by density of conspecifics. Moreover, neither biomass of substrate encrusted on the rocks nor mean mussel size appeared to have an effect on amphipod habitat partitioning.

Habitat preferences of both species were subject to significant substrate × date interactions. For example, the rank order of preferred substrates changed for both species between experiments conducted in July and August. First, in July Echinogammarus preferred Dreissena over Cladophora substrate, which itself was preferred over bare rock. By August, Cladophora was preferred less than Dreissena, but equal to bare rock.

In July, Gammarus preferred Cladophora to both bare rock and Dreissena, but selected Dreissena-encrusted rock to bare rock. By August, however, Cladophora and Dreissena were equally preferred substrates, and both were selected over bare rock.

These changes indicate a diminution in the value of Cladophora-encrusted substrate between July and August for both species. Decline of importance in Cladophora habitat was likely due to reduction in biomass in August, rendering them less complex substrates. Previous work has demonstrated that Cladophora typically experiences senescence in Lake Erie during mid- to late summer, and begins to tear-away from its epilithic

substrates (Bocsor and Judd 1972, Shear and Konasewich, 1975). This seasonal senescence of Cladophora appears to influence habitat suitability for Gammarus, and to a lesser extent, Echinogammarus.

Echinogammarus habitat preference

Echinogammarus distinctly preferred complex substrates to less complex ones, with one exception. In the August experiment, Echinogammarus selected Cladophora-encrusted rock and bare rock equally. This finding may have been due to senescence of Cladophora late in the summer (Shear and Konasewich 1975) that affected standing biomass on Cladophora-encrusted rocks. Dermott *et al.* (1998) reported Echinogammarus amongst Cladophora filaments, but the amphipod was common at only one of the three Lake Erie sites surveyed, as the other sites consisted mainly of cobble and bedrock. Rocks encrusted with small amounts of Cladophora may offer only a slight advantage to amphipods over bare rocks because animals would still be largely exposed to predation and abiotic disturbances.

Dreissena was the most preferred substrate of Echinogammarus in this study. This finding supports work by other researchers that suggested a close relationship between these two benthic species (Kohn and Waterstraat 1990, Pinkster 1993, Stewart *et al.* 1998ab, González and Downing 1999, Burkart 1999, Chapter 1). Moreover, Dermott *et al.* (1998) reported 18,000 Echinogammarus/m^2 on Dreissena-encrusted rocks at a depth of 5 m off Gibraltar Island in Lake Erie. Köhn and Waterstraat (1990) believed Echinogammarus was linked to Dreissena through their predation of ostracods that occurred in large numbers within Dreissena clumps. In this study all fauna were removed

from Dreissena-encrusted rocks prior to experimentation, thus this reason can be ruled out as the link between these species. It is more likely that Echinogammarus utilized interstitial spaces between Dreissena shells or exploited mussel feces and pseudofeces as a food source. For example, Burkart (1999) determined that feces and pseudofeces were able to sustain Echinogammarus, although growth rate was higher when they were provided macrophytes with epiphytes. More importantly, Burkart (1999) also determined that Echinogammarus was better able to avoid predation within Dreissena colonies. Although no predators were present in the aquaria during this study, this species preferred complex habitat. Even in holding tanks prior to the experiments, Echinogammarus tended to occur among complex substrate (Elodea). Echinogammarus may preferentially exploit Dreissena habitat owing to long-term co-evolution of these species in Eurasia, which has served to reduce predation risk. In this regard, introduction and spread of Dreissena in the Great Lakes may have facilitated colonization, dispersal and establishment of Echinogammarus in a manner consistent with Simberloff and Von Holle's (1999) 'invasional meltdown'.

Echinogammarus did not prefer smaller bare rocks to larger ones. This refutes Dick and Elwood (1996), who demonstrated that the marine amphipod Echinogammarus marinus preferred small stones and bare rocks (2-200 mm) to larger rocks because of increased habitat heterogeneity. Dick and Elwood (1996) also found that E. marinus tended to select larger rocks (>250 mm) with seaweed (Fucus spp.) over smaller ones. However, I observed no relationship between amphipod abundance on Cladophora-encrusted rocks and rock size. This is also contrary to findings from Chapter 1 that demonstrated Echinogammarus selects larger Cladophora rocks over smaller ones.

Biomass of Dreissena had no effect on habitat partitioning contrary to results presented in Chapter 1 that demonstrated Echinogammarus abundance increased with increasing biomass. E. ischnus did not prefer smaller Dreissena rocks to larger ones, contrary to findings in Chapter 1. These differences may be attributable to the short time span that the experiment was administered (24 hours) and/or to densities used in the experiment.

Gammarus habitat preference

Gammarus, like Echinogammarus, preferred Cladophora-encrusted rock to bare rock. Dermott *et al.* (1999) found that Gammarus occurred on both substrates, but were numerically dominant on rocks encrusted with this filamentous alga. Other researchers working in the Great Lakes region have also noted this pattern (Clemens 1950, Boscor and Judd 1972, Taft 1975, Barton and Hynes 1976, Delong *et al.* 1993, Stewart and Haynes 1994, Summers *et al.* 1997). Rocks encrusted with Cladophora may provide an advantage to Gammarus over bare rocks, particularly if algal canopy growth is prolific, because it offers refuge from predation and abiotic disturbances as well as a food source (Clemens 1950). Gammarus also preferred Dreissena-encrusted rocks over bare rocks, which is consistent with findings from many other studies (Dusoge 1966, Dermott *et al.* 1993, Griffiths 1993, Bruner *et al.* 1994, Stewart and Haynes 1994, Wisenden and Bailey 1995, Botts *et al.* 1996, Ricciardi *et al.* 1997, Beckett *et al.* 1998, Stewart *et al*, 1998ab, Strayer *et al.* 1998, Burkart 1999, Bially and MacIsaac 2000, Chapter 1).

In July, Gammarus preferred Cladophora and negatively selected Dreissena, while in August they selected the habitats equally. These differences are of interest because the amphipods selected a less complex habitat over a more complex one in July, and

preferred them equally in August. However, these differences are related to reduced vigor and biomass of Cladophora on rocks during late summer (Clemens 1950, Delong *et al.* 1993). Thus, while different habitat preferences existed, they were influenced by temporal variation in the nature of complex substrate. When Cladophora biomass was reduced from July to August *via* senescence, the preference for this substrate was lost and the amphipods switched to Dreissena substrate that afforded them greater heterogeneity than bare rock.

Size of organisms used during the experiment may also have influenced habitat selection. Large, adult Gammarus prefer filamentous algae to diatoms and animal matter, whereas juveniles prefer detritus to algae, and diatoms to animal matter as a food source (Delong *et al.* 1993, Summers *et al.* 1997). Adult amphipods used during this experiment may have preferred Cladophora habitat to Dreissena habitat because it offered a better and balanced food source (Delong *et al.* 1993). The lack of detritus on dreissenid-encrusted rocks, due to removal by agitation, may have also influenced habitat partitioning because it accounts for a very large proportion of Gammarus' diet (Delong *et al.* 1993, Summers *et al.* 1997). Equal preference of Cladophora and Dreissena in August may be related to seasonal changes in food availability or predation risk by fish (González and Downing 1999, Burkart 1999), or to senescence of Cladophora in late summer (Clemens 1950, Bocsor and Judd 1972).

Size of bare, Cladophora-encrusted or Dreissena-encrusted rocks, and Cladophora- or Dreissena-encrusted biomass were not significant determinants of habitat partitioning for Gammarus, contrary to findings in Chapter 1.

Echinogammarus and Gammarus interactions

Previous studies have predicted (Witt *et al.* 1997) or demonstrated (Dermott *et al.* 1998, Burkart 1999) replacement of Gammarus by Echinogammarus on Dreissena substrate in the Great Lakes. Mordukhai-Boltovskoi (1958, 1964) also noted displacement of freshwater amphipods by Ponto-Caspian species in the Caspian Lake. However, my study did not reveal interspecific competition on different substrates, but provided strong evidence of species-specific habitat partitioning (Gammarus on Cladophora and Echinogammarus on Dreissena). Moreover, the amphipod abundance used in both low- and high-density treatments may have failed to detect competition for Dreissena habitat because experimental animal densities were much lower than those observed under natural conditions (Chapter 1). For example, there were over 600 individuals on Dreissena-encrusted rocks of comparable area at Middle Sister Island (Chapter 1).

In summary, my laboratory experiments revealed that amphipods prefer complex to less-complex substrates, though the nature of complex substrate and amphipod preference changes seasonally. There existed clear and distinctive patterns of habitat preference for each species, though displacement of competitors was not noted on either of the substrates explored. Habitat preferences for both species were not affected by Cladophora-, or Dreissena-encrusted biomass. Finally, the establishment and rapid dispersal of Echinogammarus in the Great Lakes is likely the result of facilitation by Dreissena, a clear example of 'invasion meltdown' (Simberloff and Von Holle 1999) and in contrast to expectations based on classical species invasions theory (Elton 1958, Lodge 1993).

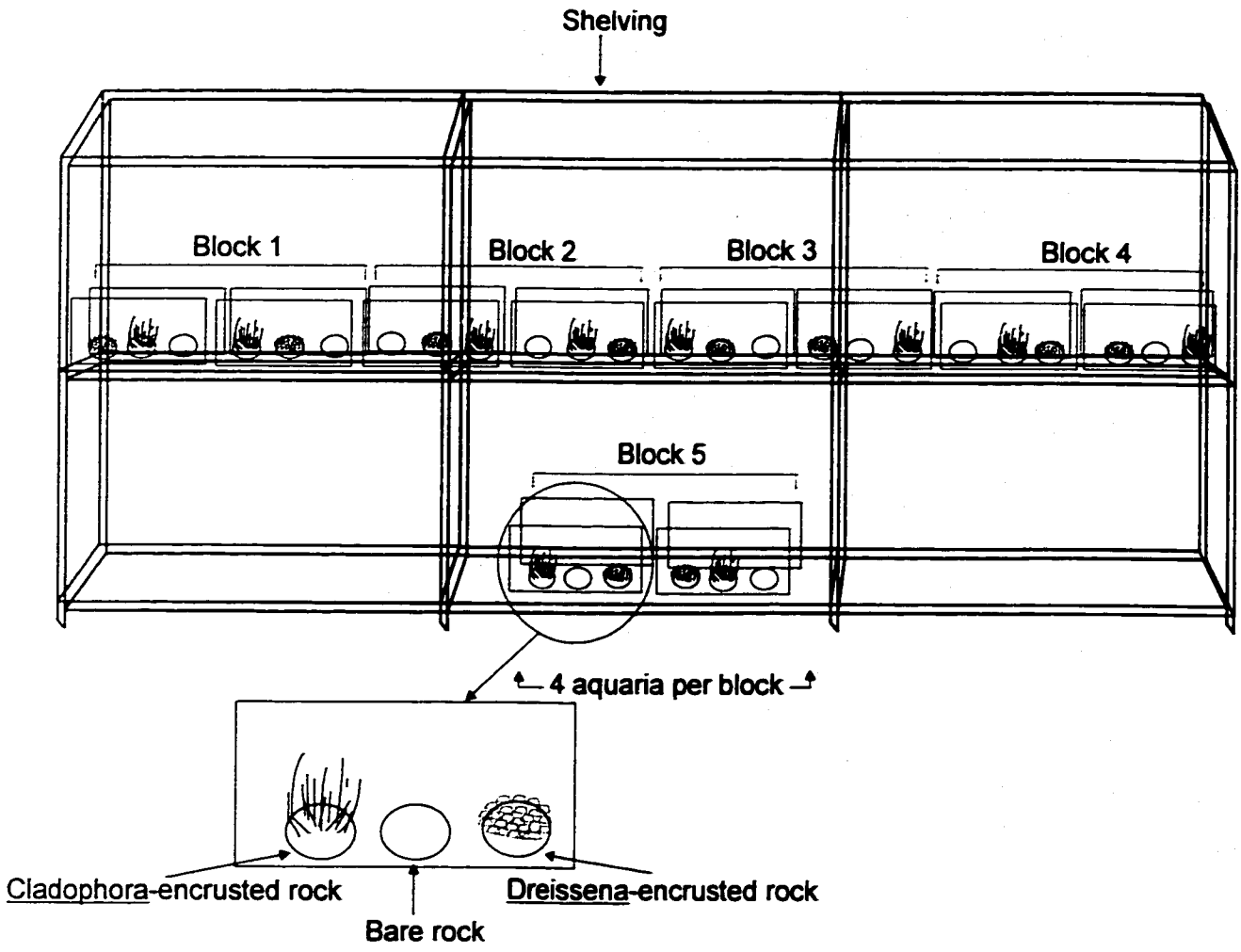


Figure 1. Experimental layout of aquaria used making up each of the five blocks. Each block contained one aquarium for each of the four treatments i) 50 Echinogammarus; ii) 50 Gammarus; iii) 25 Echinogammarus and 25 Gammarus, and iv) 50 Echinogammarus and 50 Gammarus.

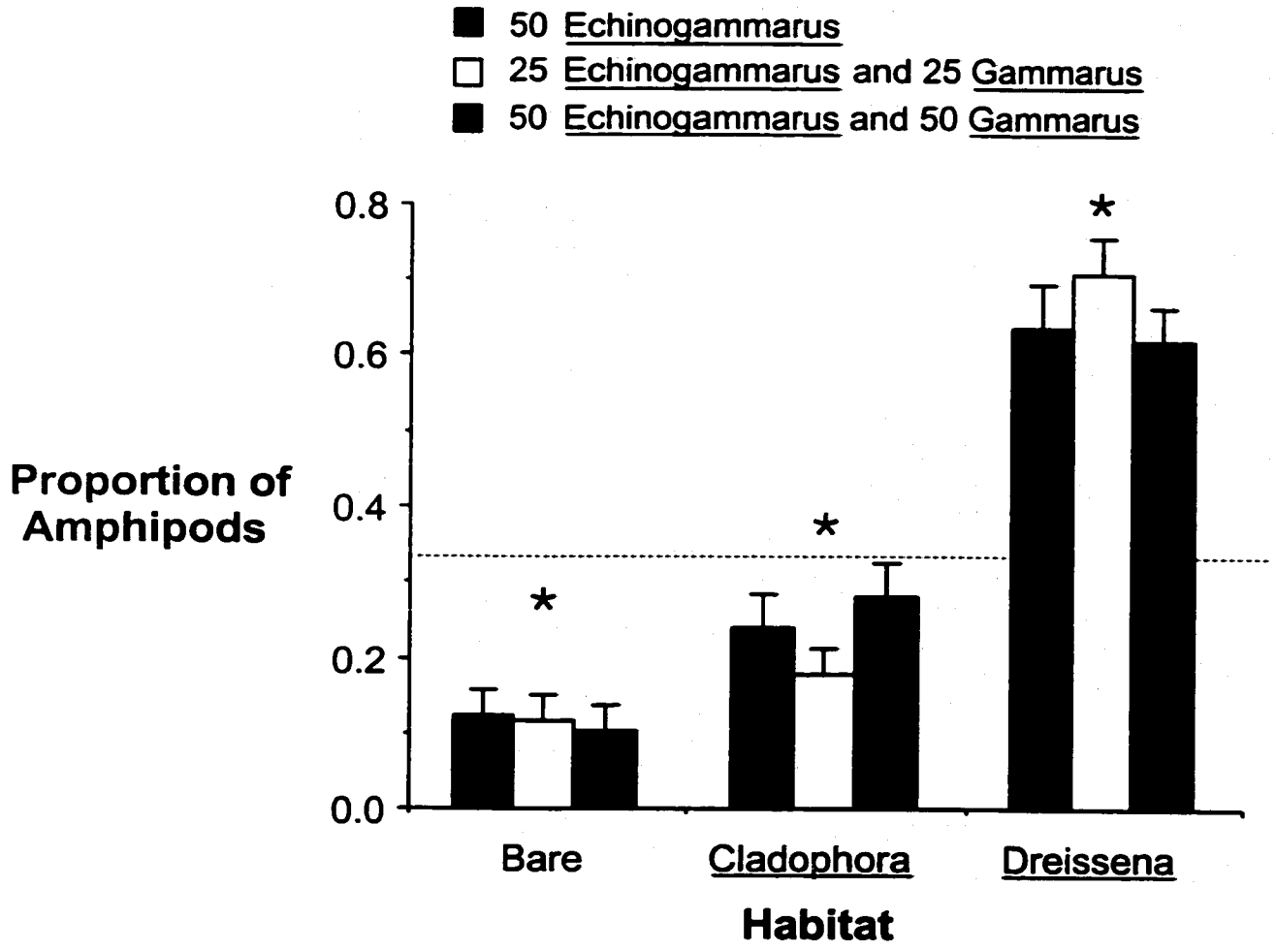


Figure 2. Mean (+SE) proportion of Echinogammarus ischnus on bare-, Cladophora- and Dreissena-encrusted rock habitat from treatments i) 50 Echinogammarus, iii) 25 Echinogammarus and 25 Gammarus, and iv) 50 Echinogammarus and 50 Gammarus from the July and August experiments. Neutral habitat selection is indicated by the dotted line. Habitats that differed significantly with respect to proportion of amphipods are indicated with an asterisk.

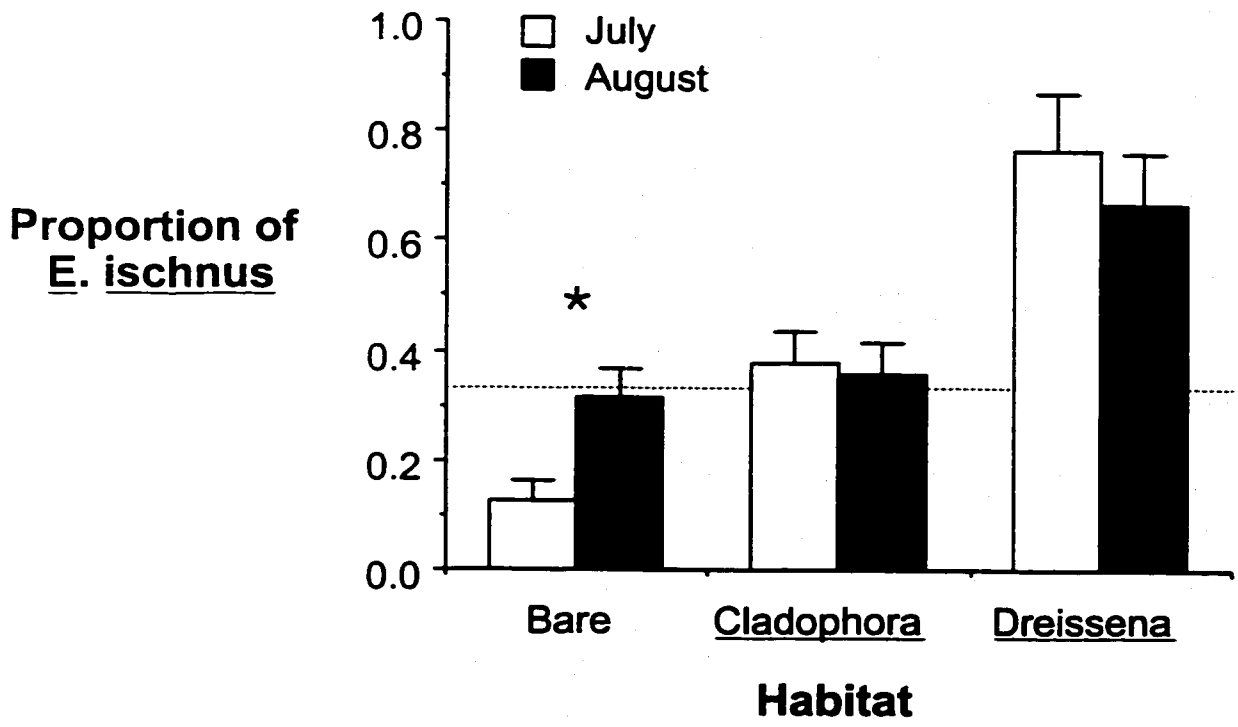


Figure 3. Mean (+SE) proportion of Echinogammarus ischnus on bare-, Cladophora-, and Dreissena-encrusted rock habitat in July and August from treatments i) 50 Echinogammarus; iii) 25 Echinogammarus and 25 Gammarus; and iv) 50 Echinogammarus and 50 Gammarus from the July and August experiments. Neutral habitat selection is indicated by the dotted line. Habitats that differed significantly with respect to proportion of amphipods are indicated with an asterisk.

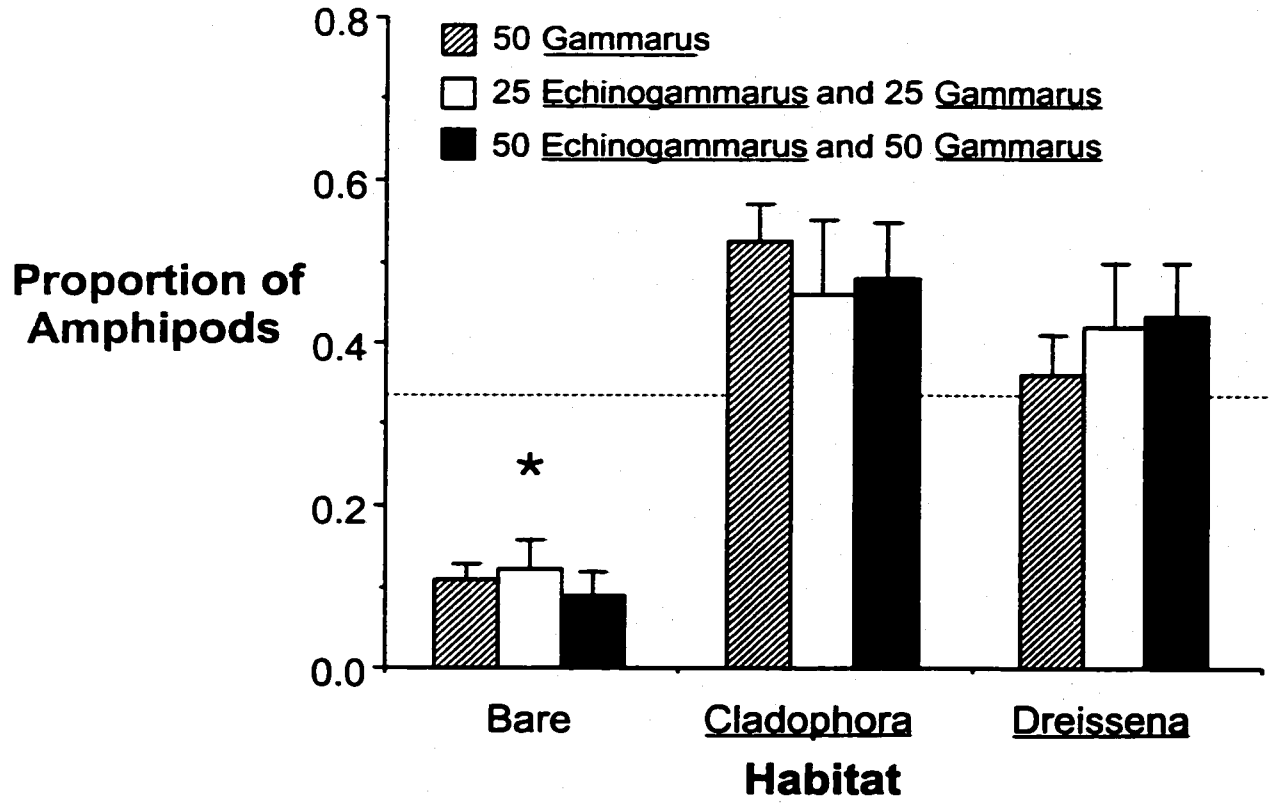


Figure 4. Mean (+SE) proportion of Gammarus fasciatus on bare-, Cladophora-, and Dreissena-encrusted rock habitat from treatments ii) 50 Gammarus, iii) 25 Echinogammarus and 25 Gammarus, and iv) 50 Echinogammarus and 50 Gammarus from the July and August experiments. Neutral habitat selection is indicated by the dotted line. Habitats that differed significantly with respect to proportion of amphipods are indicated with an asterisk.

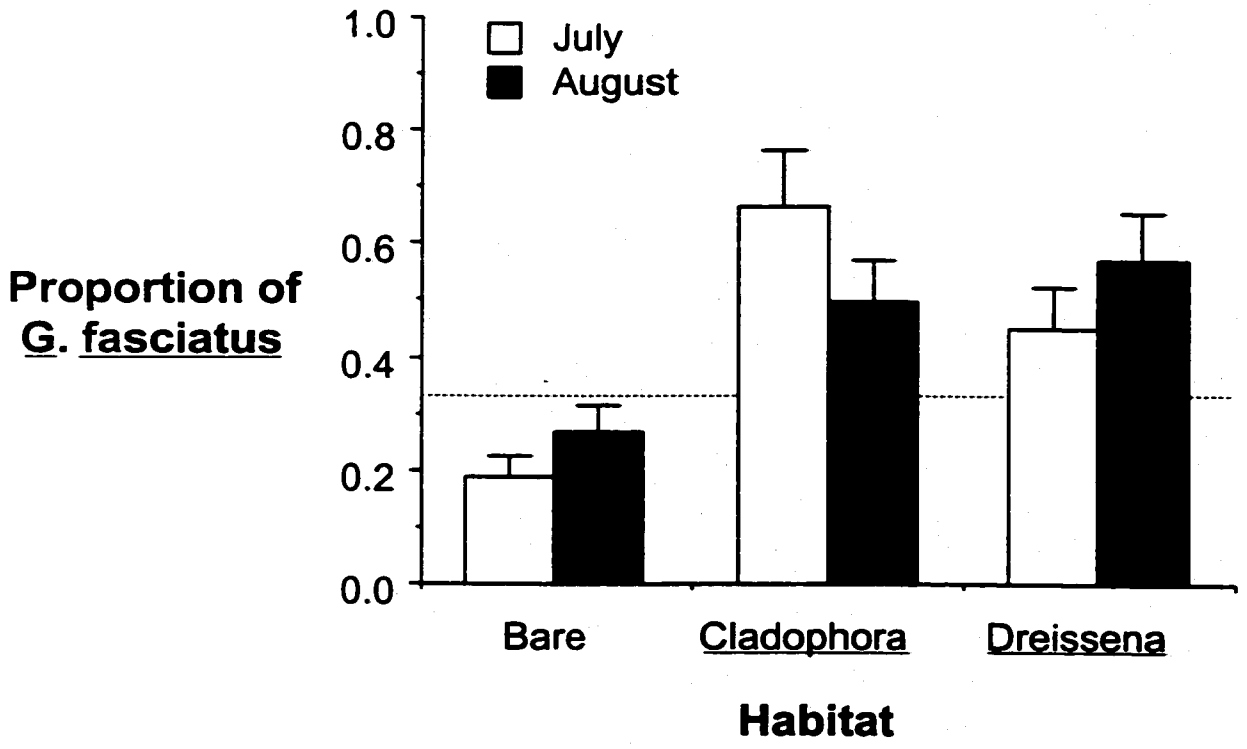


Figure 5. Mean (+SE) proportion of Gammarus fasciatus on bare-, Cladophora-, and Dreissena-encrusted rock habitat in July and August from treatments ii) 50 Gammarus, iii) 25 Echinogammarus and 25 Gammarus, and iv) 50 Echinogammarus and 50 Gammarus from the July and August experiments. Neutral habitat selection is indicated by the dotted line.

Table 1. Mean ± standard error biomass encrusted on experimental rocks and mean mussel size ± standard error for both July and August 1998.

	July 1998	August 1998
Substrate	(mg/cm^2) ± S.E.	(mg/cm^2) ± S.E
Cladophora glomerata	6.0 ± 1.0	1.0 ± 0.1
Total Dreissena spp. wet wt.	124.0 ± 8.0	73.0 ± 6.0
Mean mussel size (mm)	8.8 ± 0.3	9.6 ± 0.2

Table 2. Analysis of variance for proportional abundance of Echinogammarus ischnus (arcsine square-root) for both the July and August experiments.

Source	df	F-ratio	P
Habitat	2	131.80	< 0.001
Date	1	0.95	0.332
Treatment	2	0.05	0.950
Block	4	0.08	0.989
Habitat × Date	2	11.23	< 0.001
Treatment × Habitat	4	1.50	0.212
Error	74		

Table 3. Analysis of variance for proportional abundance of Gammarus fasciatus (arcsine square-root) for both the July and August experiments.

Source	df	F-ratio	P
Habitat	2	45.52	< 0.001
Date	1	0.12	0.735
Treatment	2	0.02	0.976
Block	4	0.03	0.999
Habitat × Date	2	8.09	< 0.001
Treatment × Habitat	4	0.43	0.784
Error	74		

Table 4. Analysis of covariance for proportional abundance of Echinogammarus ischnus (arcsine square-root) for both the July and August experiments. Habitat and treatment are independent categorical variables and rock area is the covariate.

Source	df	F-ratio	P
Habitat	2	0.09	0.912
Treatment	2	1.02	0.366
Rock area	1	0.10	0.749
Habitat × Rock area	2	2.05	0.135
Treatment × Rock area	2	1.13	0.3.28
Error	80		

Table 5. Regression analyses for proportion of Echinogammarus ischnus as the dependent variable with rock area of the three-substrate types, biomass (corrected by rock area), and mean mussel size as categorical continuous variables.

Effect	df	F-ratio	P
Bare rock	1, 28	1.13	0.297
Cladophora rock (biomass excluded)	1, 28	< 0.01	0.979
Cladophora glomerata (total wet weight)	1, 28	1.85	0.185
Dreissena rock (biomass excluded)	1, 28	2.14	0.155
Dreissena spp. (total wet weight)	1, 27	0.83	0.370
Mean mussel size	1, 28	0.04	0.841

Table 6. Analysis of covariance for proportional abundance of Gammarus fasciatus (arcsine square-root) for both the July and August experiments. Habitat and treatment are independent categorical variables and rock area is the covariate.

Source	df	F-ratio	P
Habitat	2	2.04	0.137
Treatment	2	0.08	0.922
Rock area	1	0.01	0.942
Habitat × Rock area	2	2.46	0.092
Treatment × Rock area	2	0.09	0.913
Error	80		

Table 7. Regression analyses for proportion of Gammarus fasciatus as the dependent variable with rock area of the three-substrate types, biomass (corrected by rock area), and mean mussel size as categorical continuous variables.

Effect	df	F-ratio	P
Bare rock	1, 28	0.47	0.498
Cladophora rock (biomass excluded)	1, 28	2.14	0.155
Cladophora glomerata (total wet weight)	1, 28	0.97	0.333
Dreissena rock (biomass excluded)	1, 28	0.47	0.498
Dreissena spp. (total wet weight)	1, 28	0.52	0.478
Mean mussel size	1, 28	1.93	0.176

Field Colonization Experiment

Introduction

Exotic species are a threat economically and ecologically on a global scale, and are causing a homogenization of the Earth's biota (Lodge 1993). The North American Great Lakes are among the most highly invaded aquatic ecosystems on Earth, and have become more prone to invasion by exotic species since the St. Lawrence Seaway opened in 1959 (Mills *et al.* 1993). Most of these introductions have been due to unintentional releases (29%) or from ships (29%), the latter believed to be the result of discharge of liquid (63%) or solid ballast (31%) (Mills *et al.* 1993).

The Ponto-Caspian basin (Black Sea, Azov Sea, and Caspian Lake) has been the donor region of many exotic species entering the Great Lakes (Ricciardi and MacIsaac 2000). A recent species to invade from this region is the fishhook waterflea Cercopagis pengoi that was discovered in Lake Ontario in 1998 (MacIsaac *et al.* 1999). The most recent introduction reported is by the diatom Thalassiosira baltica in Lake Ontario (Edlund *et al.* 2000).

Many Ponto-Caspian species discovered in the St. Clair River - Lake Erie corridor have greatly influenced benthic and planktonic communities. These species include the zebra mussel (Dreissena polymorpha), which was discovered in 1988 in Lake St. Clair (Hebert *et al.* 1989), the quagga mussel (D. bugensis) discovered in Lake Ontario in 1989 (May and Marsden 1992), and the round nose goby (Neogobius melanostomus) found in the St. Clair River in 1990 (Jude *et al.* 1992).

Recent studies have found that benthic crustacean fauna in the Great Lakes is of vital importance to the system's food webs (Stewart and Haynes 1994, Botts *et al.* 1996, Ricciardi *et al.* 1997, Stewart *et al.* 1998ab), and have revealed G. fasciatus as the

numerically dominant macroinvertebrate among zebra mussel colonies (Stewart and Haynes 1994, Ricciardi *et al.* 1997). Moreover, energy directed *via* Dreissena from pelagic to benthic habitats may be redirected back to commercially important fish stocks (Stewart *et al.* 1998ab) due to increased consumption of Gammarus by crayfish (Orconectes rusticus), yellow perch (Perca flavescens), rock bass (Ambloplites rupestris), and smallmouth bass (Micropterus dolomieui) (Ricciardi *et al.* 1997, Stewart *et al.* 1998b).

Echinogammarus ischnus, an amphipod native to the Ponto-Caspian basin, was discovered in the lower Detroit River in 1995 (Witt *et al.* 1997). It has recently expanded its range to lower Lake Huron and the St. Lawrence River (Dermott *et al.* 1998). This species has greatly expanded its distribution in Europe through rivers and construction of canals (Jaźdźewski 1980, Konopacka and Jesionowska 1995), and has been shown to live in close association with Dreissena in German lakes (Köhn and Waterstraat 1990). Abundance of Echinogammarus can be very high and can possibly affect abundance of G. fasciatus in the lower Great Lakes. For example, Dermott *et al.* (1998) speculated that E. ischnus was replacing G. fasciatus at sites in Lake Erie. Replacement of G. fasciatus by E. ischnus may not change structure of littoral food webs, but it has been suggested that energy transfer efficiencies could be altered (Dermott *et al.* 1998).

Echinogammarus is dorso-ventrally-compressed (Köhn and Waterstraat 1990), and may be better suited to hide from predators within interstitial spaces of Dreissena shells than Gammarus, and may be able to displace it from these areas. Thus, it is possible that

establishment and range expansion of E. ischnus may adversely affect abundance of G. fasciatus in Dreissena habitat.

The success of Ponto-Caspian species entering the Great Lakes may be related to synergistic interactions from the invasion of Dreissena that facilitated its survival and/or success, a term coined 'invasional meltdown' by Simberloff and Von Holle (1999). Therefore, rather than species introductions being decreased, as characterized by the biotic resistance model, there may be an acceleration of species introductions due to facilitation. Indeed, the establishment and rapid range expansion of E. ischnus may be related to facilitation by Dreissena. However, no mechanistic or *in situ* studies have been conducted to assess habitat preferences of invading E. ischnus, or its effects on resident amphipod species in the Great Lakes.

In this study, I examine habitat preferences of E. ischnus and G. fasciatus on substrates of varying complexity under natural conditions. Specific hypotheses tested in this chapter are that:

1) amphipod species have no preference for complex substrates (e.g. Cladophora- or Dreissena-encrusted rocks) over simple ones (bare rock);
2) amphipod habitat preferences are not affected by the presence of other potentially competing amphipod species;
3) colonization and habitation of rocky substrates are not affected by habitat quality or by lake depth.

Methods and Materials

I conducted a replicated field experiment in the western basin of Lake Erie off the east shore of Middle Sister Island (see Fig. 1; Chapter 1), a small dolomite outcrop approximately 15.7 km from the Canadian mainland (for more information see MacIsaac 1996b). The experiment ran over a three-day period from July 28-31 and from August 18-21, 1998 under natural conditions.

Experimental Design

Thirty rocks, encrusted with either Cladophora, Dreissena spp., or Dreissena spp. with attached Cladophora (Dreissena + Cladophora) were collected at the study site from 0.5, 2.5 and 2.0 m depths, respectively, using snorkel or SCUBA, sealed underwater in polypropylene bags (large Ziploc® freezer bags) and brought to the surface. Five rocks of each substrate type were randomly selected and fixed with 5% sugar-formalin solution to determine initial amphipod abundance (control I). Remaining rocks were agitated in a bucket of Lake Erie water for 2 minutes to dislodge existing amphipods. An additional five rocks of each substrate type were randomly selected and fixed with 5% sugar-formalin to determine amphipod abundance prior to transplantation (control II).

A transect perpendicular to shore was fixed and depths of 0.5, 1.0, 1.5, 2.0 and 2.5-m were marked with buoys. The site consisted mainly of bedrock, cobble encrusted with Cladophora and/or Dreissena, and a few macrophytes (Vallisneria). Sixteen rocks (four of each substrate type, and four bare rocks brought on site) were randomly selected from the pool of shaken rocks, sealed in polypropylene bags, brought to the marked depths,

and arranged into a Latin square design using snorkel or SCUBA. Fluorescent painted rocks were placed at each depth on two sides of the square to aid in reclamation (Fig. 1). After approximately 72 hours, rocks were collected by snorkel or SCUBA, placed into marked polypropylene bags, sealed underwater, brought to the surface and fixed immediately with 5% sugar-formalin.

Laboratory Analysis

All rocks (including controls) were scraped clean with a surgical blade and material saved in separate, marked 500 mL mason jars and preserved in 5% sugar-formalin. Fauna collected on the rocks was passed through a series of sieves with different mesh sizes (4 mm, 1 mm, 500 μm, 250 μm, and 125 μm), separated into dense and buoyant matter by the 'gold panning technique' (Ciborowski 1992) and placed into Petri dishes. E. ischnus and G. fasciatus were identified and sorted, using descriptions from Witt *et al.* (1997), under a dissecting microscope (Zeiss Jena, model Technival 2) at 5 X magnification, counted, and preserved in 5% sugar-formalin solution.

Volume of rocks used in the experiment was assessed using the water displacement technique, with three measures taken for each rock and the mean calculated. Volume of rocks was then converted to area (cm^2) from surface area-rock volume correlations calculated by MacIsaac (1996b). Dreissena samples were cleaned by removing broken shells and byssal threads, sorted by species, blotted dry, and mass recorded on an AND FX-200 electronic balance. D. polymorpha right valve lengths were measured to the nearest 0.1 mm using Manostat (model # 15-100-500) vernier calipers using the sub-sampling technique described in MacIsaac (1996b) for 100 individuals. All D. bugensis

right valve lengths were measured. D. polymorpha and D. bugensis dry weights were determined by placing mussels on pre-weighed, dried aluminum boats (60°C, 24 hr) in an oven for 48 hours at 60° C. Cladophora wet weight was determined on the electronic balance after filaments were compressed between paper towels to remove excess water.

Statistical Analysis

Shaken rocks (control II) still contained individuals of both amphipod species before the rocks were deployed in the experiments. Therefore, I analyzed each species' abundance on control II rocks separately with Dixon's outliers test (Dunn and Clark 1974) on all three substrates and for both experimental dates. Gammarus abundance remaining on all three encrusted substrate types and Echinogammarus abundance remaining on Cladophora-encrusted treatment was non-significant at each date. However, Echinogammarus abundance remaining on one of each of the five rocks (control II) for Dreissena, and Dreissena + Cladophora treatments were significant for both dates. This outlier was omitted, and the mean amphipod abundance was calculated for each species on all three treatments, and for both experimental dates from the four remaining rocks. Mean amphipod abundance, after shaking, on each treatment was subtracted from the original abundance initially encountered on investigation rocks. Adjusted amphipod numbers for both species were divided by the rock area on which it was present, and log (x + 1) transformed prior to analysis in Systat (Version 8.0).

Statistical Tests

Variation in rock area was determined by 3-way ANOVA with rock area as the dependent variable and with treatment, date and depth entered as independent categorical variables. A date × treatment interaction effect was also included in the model.

To determine whether substrate biomass varied between experimental dates, separate 3-way ANOVA's were conducted for Cladophora and both Dreissena treatments. Corrected wet weight biomass (biomass divided by rock area) was entered as the dependent variable and treatment, date and depth as independent categorical variables. A separate 3-way ANOVA was also conducted on mean mussel size encrusted on the rocks. Mussel size served as the dependent variable and treatment, date and depth as independent categorical variables.

A multiple analysis of variance (3-way MANOVA) was utilized to determine the effects of treatment, date and depth on amphipod abundances. Transformed amphipod abundances of both species were entered as the dependent variables and treatment, date and depth as the independent categorical variables. Treatment × depth, and treatment × date interaction effects were also included in the model.

Separate general linear models (3-way ANCOVA) were conducted on each amphipod species to determine main effects within the MANOVA. Transformed amphipod abundance was entered as the dependent variable, and treatment, date, and depth as independent categorical variables. Treatment × depth and treatment × date interaction effects were also included in the model. Bonferroni multiple comparisons test (at $\alpha <$

0.05) were utilized to explore the nature of the differences. Transformed amphipod abundance values of the interspecific amphipod species were entered as the covariate.

To determine effects of rock area, biomass encrusted on experimental rocks, and mean mussel size on amphipod habitat preference, separate linear regressions were conducted. The transformed abundance of each amphipod species was entered as the dependent variable and either rock area of each treatment, or Cladophora and Dreissena total wet weight biomass, or mean mussel size encrusted on rocks entered as the independent continuous variables.

Results

Substrates

Rock area differed between the four rocky treatments ($F = 4.64$, $df = 3, 133$, $p = 0.004$), experimental dates ($F = 13.06$, $df = 1, 133$, $p < 0.001$), and by depth ($F = 8.18$, $df = 4, 133$, $p < 0.001$). However, there were no significant date × treatment interactions ($F = 1.62$, $df = 3, 133$, $p = 0.187$). Rocks encrusted with Dreissena, and Dreissena + Cladophora were smaller than bare rocks (Bonferroni's test). Moreover, rocks were smaller in August than in the July experiment (Bonferroni's test). Depth effects revealed rocks were larger at the 1.5 and 2.0 m depths than at the 1.0 m depth, and were smaller at 2.5 m than at the 2.0 m depth (Bonferroni's test).

Cladophora-encrusted biomass on rocks varied among treatments ($F = 14.21$, $df = 2, 100$, $p < 0.001$) and between experimental dates ($F = 23.03$, $df = 1, 100$, $p < 0.001$), but not among depths ($F = 1.35$, $df = 4, 100$, $p = 0.256$). Algal biomass was lower on

Dreissena- and Dreissena + Cladophora-encrusted rocks than on Cladophora-encrusted rocks (Bonferroni test). Although algal biomass was higher on Dreissena + Cladophora treatments than on plain Dreissena (Table 1), they did not differ statistically (Bonferroni's test). Cladophora-encrusted biomass was also significantly lower in August than in July (Bonferroni's test). For example, Cladophora-encrusted rocks contained an average of 3 mg/cm^2 of algal biomass during July, but only 1 mg/cm^2 during August (Table 1).

Dreissena-encrusted biomass differed between both Dreissena treatments ($F = 8.98$, $df = 1, 67$, $p = 0.004$) and between experimental dates ($F = 6.20$, $df = 1, 67$, $p = 0.015$), but not among depths ($F = 1.66$, $df = 4, 67$, $p = 0.170$). Mussel biomass was lower on Dreissena + Cladophora-encrusted rocks than on Dreissena-encrusted rocks (Bonferroni's test) (Table 1). Mussel biomass was also lower in August than in the July experiment (Bonferroni's test) (Table 1).

Average mussel size differed between Dreissena treatments ($F = 25.06$, $df = 1, 67$, $p < 0.001$), but did not differ between experimental dates ($F = 0.12$, $df = 1, 67$, $p = 0.730$) or by depth ($F = 0.79$, $df = 4, 67$, $p = 0.535$; Table 1). Mussel sizes were smaller on Dreissena + Cladophora-encrusted rocks than on Dreissena-encrusted rocks (Bonferroni's test). Species composition on rocks with mussels was 95 % D. polymorpha and 5 % D. bugensis (wet weight). Wet and dry mussel mass including shells, was highly correlated (Pearson's $r = 0.999$).

Echinogammarus and Gammarus Habitat Preference

Treatment effects

There were significant treatment, date, depth, treatment × depth, and treatment × date interactions with both amphipod species (MANOVA; Table 2). Echinogammarus abundance varied among the different treatments (Univariate test; Table 2). Its abundance was higher on the Dreissena and Dreissena + Cladophora treatments than on both bare and Cladophora treatments, but abundance on both Dreissena treatments was equal (Fig. 2). Moreover, abundance was equivalent on both bare and Cladophora-encrusted rocks (Fig. 2). Thus, the rank order of Echinogammarus abundance on experimental rocks was Dreissena (48 %), Dreissena + Cladophora (47 %), Cladophora (4 %) and bare (1 %).

Gammarus' abundance also varied among the different treatments (Univariate test; Table 2). Its abundance was higher on the Dreissena treatment than on both bare and Cladophora treatments, and was equal among the bare, Cladophora and Dreissena + Cladophora treatments (Fig. 2). However, its abundance was significantly lower on the Dreissena + Cladophora treatment than on the Dreissena treatment (Fig. 2). The rank order of Gammarus abundance was Dreissena (50 %), Dreissena + Cladophora (30 %), Cladophora (15 %) and bare (5 %). Overall abundance for both amphipod species also followed this pattern, 49 % of the amphipods occurred on Dreissena, 42 % on Dreissena + Cladophora, 5 % on Cladophora and 4 % on the bare rock treatment.

Depth effects

Echinogammarus abundance clearly displayed patterns associated with depth (Univariate test; Table 2). Abundance was greater at the 1.0-m depth than at the 0.5-m depth, and there were significantly fewer Echinogammarus at the 1.5, 2.0 and 2.5-m depths than at the 1.0-m depth (Fig. 2). Echinogammarus abundance was higher at the shallower depths than at the deeper depths, but was highest at the 1.0-m depth. Thus, the rank order of Echinogammarus abundance by depth was 1.0-m (46 %), 2.0-m (19 %), 0.5-m (14 %), 1.5-m (12%) and the 2.5-m depth (10 %).

Gammarus also displayed abundance patterns associated with depth (Univariate test; Table 2). Numbers were not significantly different between the 0.5 and 1.0-m depths, however, there were fewer amphipods at the 1.5, 2.0 and 2.5-m depths that at the 0.5-m depth, and fewer at the 2.5-m depth than at the 1.0-m depth (Fig. 2). Gammarus abundance, like Echinogammarus', was higher at the shallower depths than at the deeper ones. The rank order of Gammarus abundance by depth was 1.0-m (29 %), 0.5-m (27 %), 2.0-m (22 %), 1.5-m (17 %) and the 2.5-m depth (6 %).

Treatment × depth interaction effects

Echinogammarus abundance at the 0.5, 1.5 and 2.5-m depths were significantly higher on the Dreissena treatment over both bare and Cladophora treatments, but was equal to the Dreissena + Cladophora treatment (Univariate test Table 2; Fig. 2). Moreover, Echinogammarus abundance was equal between the bare, Cladophora and Dreissena + Cladophora treatments at these depths. However, at the 1.0-m depth,

Echinogammarus abundance was higher on both Dreissena and Dreissena + Cladophora than on the bare and Cladophora treatments, but abundances were equal between both Dreissena treatments (Fig. 2). Echinogammarus abundance was higher on the Dreissena + Cladophora treatment over both bare and Cladophora treatments at the 2.0-m depth, but there were no differences among Dreissena treatments or between the Dreissena, bare and Cladophora treatments (Fig. 2).

Gammarus abundance was higher on the Dreissena treatment over both bare and Cladophora treatments at the 0.5-m depth, and was equal to the Dreissena + Cladophora treatment (Univariate test Table 2; Fig. 2). There was no difference in Gammarus' abundance between the bare, Cladophora and Dreissena + Cladophora treatments at the 0.5-m depth. Gammarus abundance was significantly greater on the Dreissena treatment over all other treatments, but there was no difference between the bare, Cladophora and Dreissena + Cladophora treatments at the 1.0-m depth (Fig. 2). At the 1.5 and 2.0-m depths, Gammarus abundance was only greater on the Dreissena treatment over the bare rock treatment, no other significant treatment interactions occurred (Fig. 2). Gammarus abundance was equal among all four treatments at the 2.5-m depth (Fig. 2).

Date and Treatment × date effects

Echinogammarus abundance was 220 % higher in July than in August, while Gammarus abundance decreased 36 % over the same time interval (Univariate tests; Table 2). Both amphipod species were also subject to treatment × date interactions (Univariate tests; Table 2). Echinogammarus abundance did not change significantly on

Cladophora or Dreissena treatments from July to August, however, its abundance increased significantly on both bare and Dreissena + Cladophora treatments from July to August (Fig. 3).

Gammarus abundance did not differ between bare or Dreissena + Cladophora treatments from July to August, but its abundance decreased significantly on both Cladophora and Dreissena treatments from July to August (Fig. 4).

The interaction between amphipod species was non-opposing, and had a positive effect. The presence of one amphipod species tended to increase the abundance of the other species (Fig. 5).

Hyalella habitat preference

Hyalella were also detected during the course of the experiments, but its abundance remained very low. Hyalella did not display any treatment relationships, but there were fewer animals at the 1.5, 2.0 and 2.5-m depths than at the 0.5-m depth.

Rock area, Biomass and Mussel Size Effects on Amphipod Habitat Preference

Rock area and biomass of Cladophora did not affect Echinogammarus abundance on experimental rocks (Table 3). However, Dreissena biomass (Fig. 6; Table 3) and mean mussel size (Fig. 7; Table 3) had significant positive effects on Echinogammarus' abundance.

Gammarus abundance was not related to mean size of mussels encrusted on rocks, or by rock area (Table 4). However, Dreissena- (Fig 6; Table 4) and Cladophora-encrusted biomass (Fig. 8; Table 4) had significant positive effects on Gammarus' abundance.

Discussion

My results indicate that amphipods have strong tendencies to select complex rocky substrates in western Lake Erie over more simple ones. Moreover, depth and season tend to influence abundance patterns of each species on these habitat types. This is the first study to specifically examine Echinogammarus and Gammarus habitat preferences in a field setting. González and Downing (1999) examined amphipod habitat choices in Lake Erie, but they did not differentiate habitat preferences of each species separately, and reported a combined response. They also did not include Cladophora-encrusted habitats that are available to amphipods in littoral areas in western Lake Erie. González and Downing (1999) reported that amphipods only preferred complex substrates to bare rocks in late summer (August), but not earlier in the season (June and July). Contrary to their study, I found that both amphipod species preferred complex substrates to bare rock in both July and August.

Both amphipod species selected Dreissena- to bare and Cladophora-encrusted rocks, and each species equally selected bare and Cladophora-encrusted rocks. However, the two species displayed some differences with respect to their selection of rocks attached with both Dreissena and Cladophora. Echinogammarus preferred Dreissena + Cladophora-encrusted rocks over both bare and Cladophora-encrusted rocks, and equally selected both Dreissena treatments. Gammarus density was equal between bare, Cladophora- and Dreissena + Cladophora-encrusted rocks, and was significantly lower on Dreissena with filamentous algae than Dreissena without it. Habitat preferences of both species were unaffected by the presence of heterospecifics. Thus, while each species demonstrated habitat preferences, these selections were not influenced by the presence of

heterospecific individuals. Moreover, while competitive interactions were not noted among amphipod species on different habitats, there was a positive trend of amphipod abundance in the presence of heterospecifics across all four rocky treatments. It is important to note, however, that the short-term field densities reported here are far lower than natural field densities. Thus, the potential for competitive interactions may be commensurately reduced.

Echinogammarus and Gammarus abundance was positively affected by Dreissena biomass encrusted on rocks. Biomass of Cladophora encrusted on rocks had a positive effect on Gammarus abundance, but not on abundance of Echinogammarus.

The size of mussels encrusted on rocks had a positive effect on Echinogammarus abundance, but not on Gammarus abundance. Thus, Echinogammarus responded positively to both mussel mass and to the size of mussels encrusted on rocks, whereas Gammarus, responded only to the biomass of either substrate.

Time of season had an effect on amphipod abundance. Echinogammarus abundance increased from July to August (Fig. 3), while Gammarus abundance decreased over this time interval (Fig. 4). Increased abundance of Echinogammarus from July to August is possibly related to their third reproductive period, which peaks during this time interval (Köhn and Waterstraat 1990, Konopacka and Jesionowska 1995). Decreased abundance of Gammarus was possibly due to increased depletion of large individuals, which occurs during this time (Clemens 1950).

Amphipod abundances were also affected by depth. Abundance of both amphipod species was lower at the deeper depths (1.5, 2.0, and 2.5 m) than at the shallower sites (0.5 and 1.0 m). Moreover, even at these shallower depths each amphipod species

abundance varied. Echinogammarus was more abundant at 1.0 m than at 0.5 m, while Gammarus abundance did not vary between the two depths.

Köhn and Waterstraat (1990) reported Echinogammarus had a preferred habitat between 0 and 2 m in German lakes, while various researchers in the Great Lakes reported Gammarus had a preferred habitat less than 2.0 m (Ricciardi *et al.* 1997) and up to 9.1 m depth (Bially and MacIsaac 2000).

Kuhns and Berg (1999) have reported that presence of round nose goby (Neogobius melanostomus) in Lake Michigan decreased non-mussel invertebrate densities by 44%, and gobies had an adverse affect on Gammarus' abundance. Similarly, other researchers in the Great Lakes have reported that gobies primarily consume amphipods (Jude and Deboe 1996, Dubs and Corkum 1996). Moreover, Shorygin (1952) reported that juvenile round nose gobies eat 34% by weight of their diet on gammarid amphipods in their native home range. Thus, restriction of both species of amphipod to shallow depths may be related to presence of gobies.

Abundance of both amphipod species was subject to significant habitat × date interactions. For example, Echinogammarus abundance increased significantly on both bare rock and Dreissena + Cladophora-encrusted rocks during the August experiment, while abundance did not change on Cladophora- and Dreissena-encrusted rocks between July and August (Fig. 3). Gammarus abundance decreased significantly in August on both Cladophora- and Dreissena-encrusted rocks, while abundance on bare rock and Dreissena + Cladophora-encrusted rock did not change between July and August (Fig. 4). Decreased abundance of Gammarus on Cladophora-encrusted rocks in August is likely

related to the diminution of Cladophora on the rocks due to senescence, thereby rendering them less complex substrates (Shear and Konasewich 1975, Chapter 2). For example, Cladophora biomass declined by 78 % between July and August. Increased Echinogammarus abundance on Dreissena + Cladophora-encrusted rocks may also be related to senescence of Cladophora.

Echinogammarus habitat preference

Echinogammarus distinctly preferred complex substrates to less complex ones. Dreissena-encrusted rocks were the most preferred substrate for this amphipod during this study. This finding supports work by other researchers that suggested a close relationship between these two Ponto-Caspian species (Köhn and Waterstraat 1990, Pinkster 1993, Konopacka and Jesionowska 1995, Stewart *et al.* 1998 a, González and Downing 1999, Burkart 1999, Chapter 1, Chapter 2). For example, Dermott *et al.* (1998) reported Echinogammarus as the dominant amphipod on Dreissena substrate at the Leamington Marina in Lake Erie. Echinogammarus could potentially derive two benefits from living in amongst Dreissena shells. First, they may be less vulnerable to predators in this habitat (González and Downing 1999, Burkart 1999). Alternatively, they may experience higher food concentrations (Köhn and Waterstraat 1990). For example, Burkart (1999) determined that feces and pseudofeces were able to sustain Echinogammarus living within Dreissena colonies.

Echinogammarus appears to preferentially exploit Dreissena habitat owing to long-term co-evolution of these species in Eurasia, which serves to reduce predation risk (Köhn and Waterstraat 1990, Pinkster 1993, Konopacka and Jesionowska 1995). In this

regard, introduction and spread of Dreissena in the Great Lakes appears to have facilitated colonization, establishment and dispersal of Echinogammarus in a manner consistent with Simberloff and Von Holle's (1999) 'invasional meltdown' hypothesis.

Echinogammarus density was not affected by rock size. This finding is contrary to those of Dick and Elwood (1996), who demonstrated that the marine amphipod Echinogammarus marinus preferred small stones and bare rocks (2-200 mm) to larger rocks, but supports evidence from Chapter 2. Dick and Elwood (1996) also found that E. marinus tended to select larger rocks (>250 mm) fouled by seaweed (Fucus spp.) over smaller ones. Nonetheless, I observed no relationship between Echinogammarus abundance on Cladophora-encrusted rocks and rock size, consistent with my findings from Chapter 2, but contrary to my findings in Chapter 1, where it preferred larger Cladophora-encrusted rocks.

However, Echinogammarus habitat partitioning on Dreissena-encrusted substrate had significantly positive relationships to mussel size and total Dreissena biomass, contrary to my findings in Chapter 2.

Gammarus habitat preference

Relative to bare rock, Gammarus had significantly higher densities on most complex substrates, and the highest density on Dreissena-encrusted rock. The latter finding is consistent with results from many other studies (Dusoge 1966, Dermott *et al.* 1993, Griffiths 1993, Bruner *et al.* 1994, Stewart and Haynes 1994, Wisenden and Bailey 1995, Botts *et al.* 1996, Ricciardi *et al.* 1997, Beckett *et al.* 1998, Stewart *et al*, 1998ab, Strayer *et al.* 1998, Burkart 1999, Bially and MacIsaac 2000, Chapter 1, Chapter 2). Like

Echinogammarus, Gammarus utilizes interstitial spaces between Dreissena shells as refuge from predators and abiotic disturbances (Botts *et al.* 1996, Stewart *et al.* 1998ab). To a lesser extent, Gammarus benefits from feces and pseudofeces produced by Dreissena (Griffiths 1993, Dermott *et al.* 1993, Stewart and Haynes 1994, Wisenden and Bailey 1995, Botts *et al.* 1996, Ricciardi *et al.* 1997, Stewart *et al.* 1998ab, Kuhns and Berg 1999, Bially and MacIsaac 2000).

Density of Gammarus was similar on bare rock, Cladophora-encrusted rock and rocks encrusted with Dreissena + Cladophora (Fig. 2). The only treatment that supported higher densities of Gammarus was that of Dreissena-encrusted rocks. Gammarus did not respond positively to treatments with Cladophora. This finding is contrary to evidence from other studies on the Great Lakes that have noted Gammarus on rocks encrusted with Cladophora (Clemens 1950, Taft 1975, Delong *et al.* 1993, Stewart and Haynes 1994, Summers *et al.* 1997, Dermott *et al.* 1999, Chapter 1, Chapter 2). While this study failed to uncover positive effects of treatments with Cladophora, Gammarus abundance was positively correlated with Cladophora biomass on individual rocks (Fig. 8).

Gammarus density was not related to rock size. These findings run contrary to results of my laboratory experiment (Chapter 1), where it preferred larger Dreissena-encrusted rocks to smaller ones.

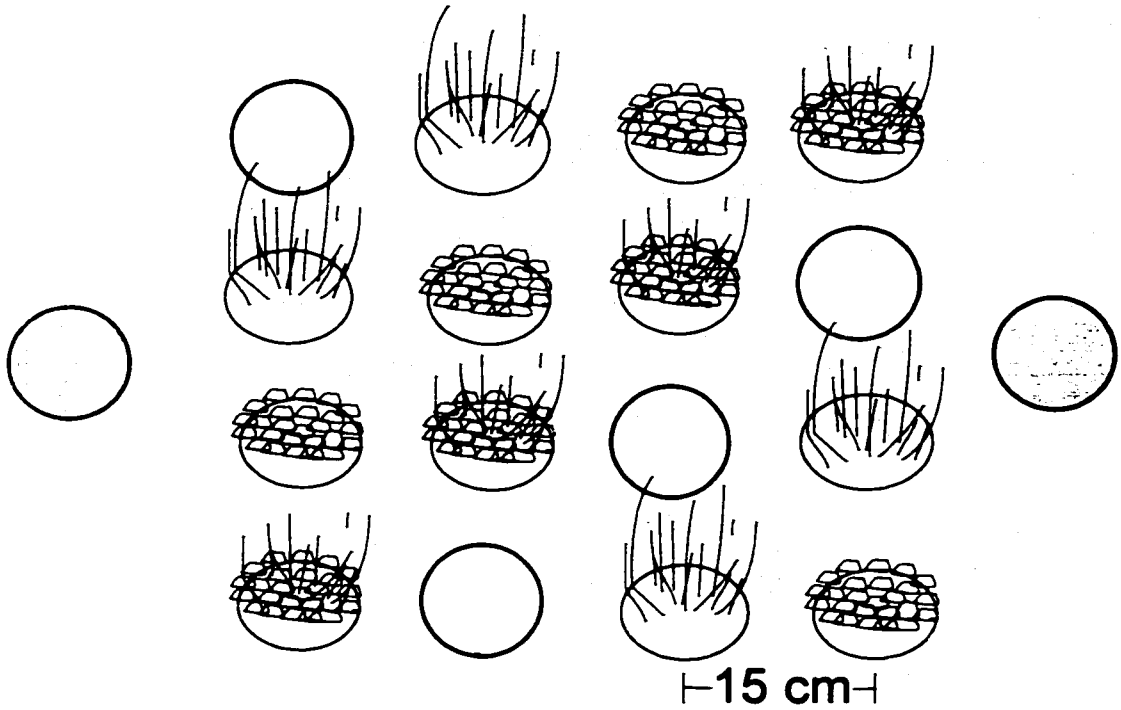
Echinogammarus and Gammarus interactions

Previous studies have predicted (Witt *et al.* 1997) or demonstrated (Dermott *et al.* 1998, Burkart 1999) replacement of Gammarus by Echinogammarus on Dreissena substrate in the Great Lakes. Moreover, Mordukhai-Boltovskoi (1958, 1964) noted

displacement of freshwater amphipods by Ponto-Caspian species in the Caspian Lake. However, my study did not reveal interspecific competition, but rather provided weak evidence for a positive relationship between densities of these amphipod species. However, this may be an artifact as abundances of both species are much lower than those recorded from natural field densities (Chapter 1). Both species appeared to prefer Dreissena-encrusted rocks, with preference being slightly stronger for Echinogammarus.

In summary, my field experiments revealed that both Echinogammarus ischnus and Gammarus fasciatus prefer complex to less-complex substrates, and that abundances of each species on these substrates change by depth and by season. Subtle patterns of habitat preference existed with Echinogammarus on all substrates containing Dreissena, while Gammarus density was higher only on Dreissena-encrusted rocks. On individual rocks, Gammarus responded to Cladophora biomass. There was no evidence of competition between amphipod species, rather, densities of the two species were weakly, but positively correlated. Senescence of Cladophora in late summer affected abundance of Gammarus on Cladophora-encrusted rocks, and Echinogammarus abundance on Dreissena + Cladophora-encrusted rocks. Establishment and rapid dispersal of Echinogammarus in the Great Lakes is likely the result of facilitation by Dreissena, a clear example of 'invasion meltdown' (Simberloff and Von Holle 1999).

Figure 1. Experimental design of substrates used at each of the five depths (0.5, 1.0, 1.5, 2.0, 2.5 m) along the transect at Middle Sister Island. Each block contained four rocks of each substrate type in a Latin Square design i) Bare rock; ii) Cladophora-encrusted rock; iii) Dreissena-encrusted rock, and iv) Dreissena + Cladophora-encrusted rock.



Legend

Bare rock

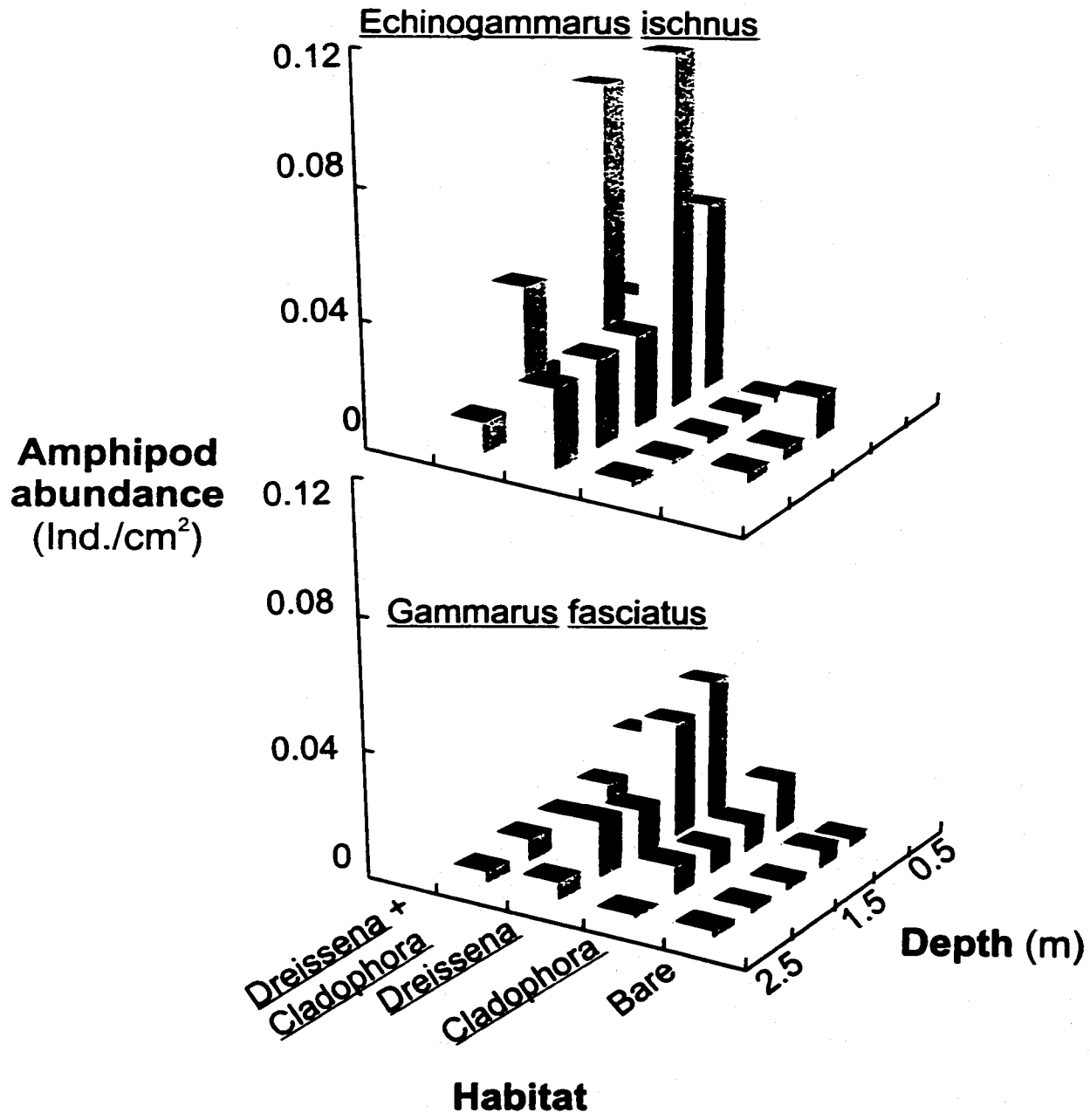
Cladophora-encrusted rock

Dreissena-encrusted rock

Dreissena + Cladophora encrusted rock

Flourescent marker

Figure 2. Mean abundance of colonizing Echinogammarus ischnus and Gammarus fasciatus on bare, Cladophora-, Dreissena-, and Dreissena + Cladophora-encrusted rocks near Middle Sister Island.


Echinogammarus ischnus
0.12
0.08
0.04
0
Amphipod abundance (Ind./cm²)
0.12
0.08
Gammarus fasciatus
0.04
0
Dreissena + Cladophora
Dreissena
Cladophora
Bare
0.5
1.5
2.5
Depth (m)
Habitat

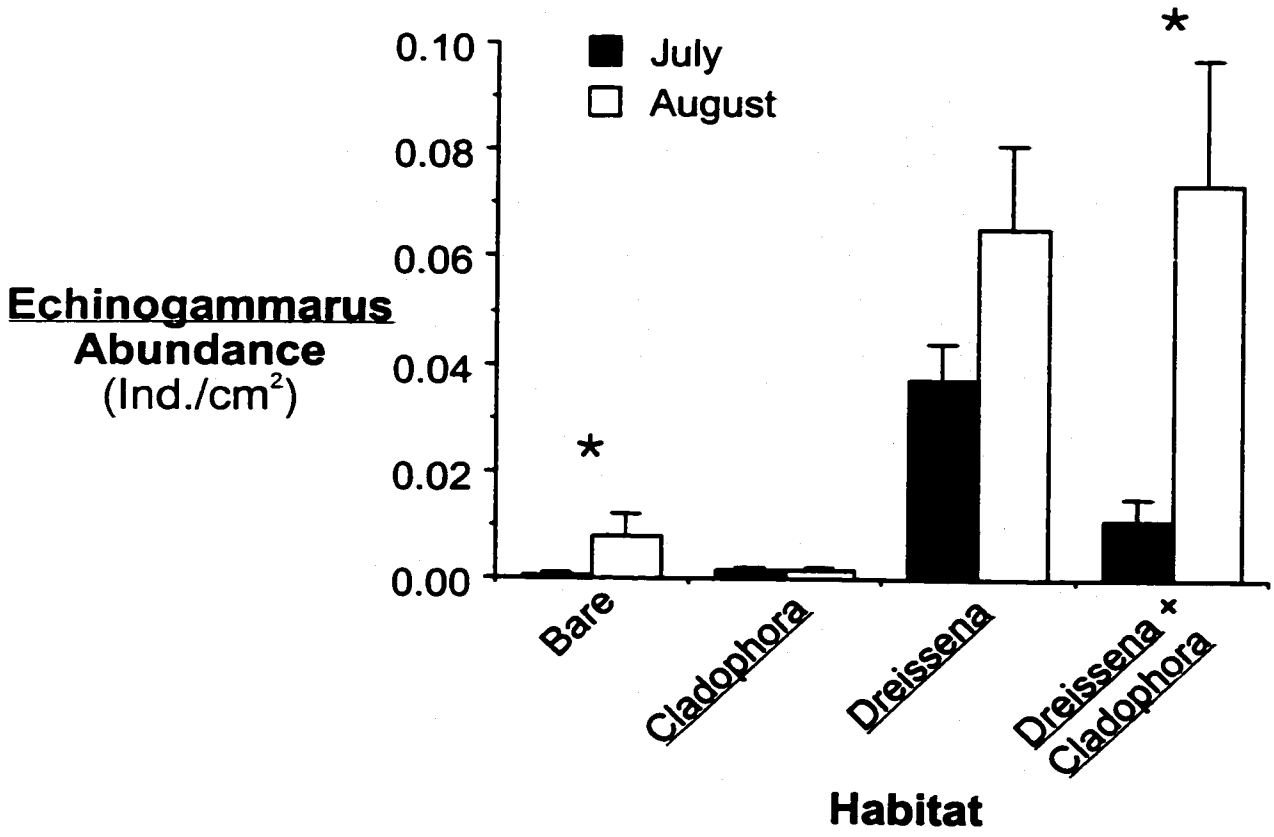


Figure 3. Mean (+SE) abundance of Echinogammarus ischnus (Ind./cm^2) on bare, Cladophora-, Dreissena, and Dreissena + Cladophora-encrusted rock from the July and August experiments. Habitats that differed significantly with respect to proportion of amphipods are indicated with an asterisk.

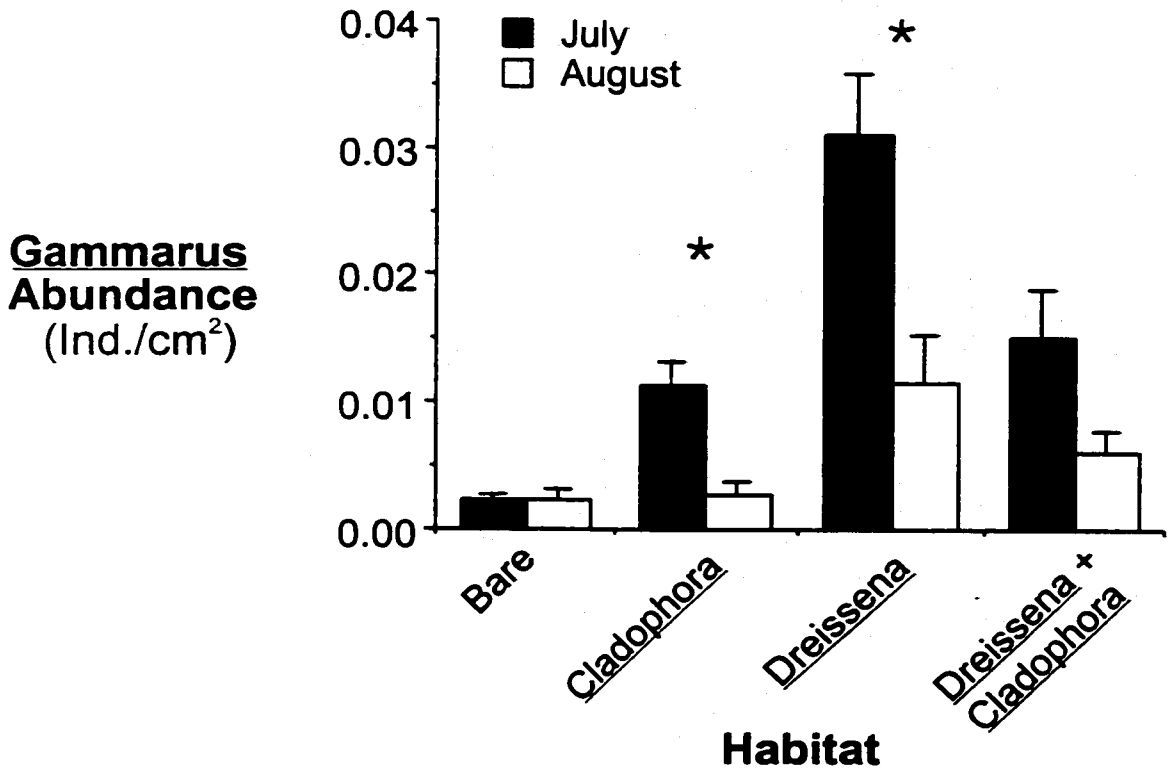


Figure 4. Mean (+SE) abundance of Gammarus fasciatus (Ind./cm^2) on bare, Cladophora-, Dreissena, and Dreissena + Cladophora-encrusted rock from the July and August experiments. Habitats that differed significantly with respect to proportion of amphipods are indicated with an asterisk. Note change in y-axis scale from Figure 3.

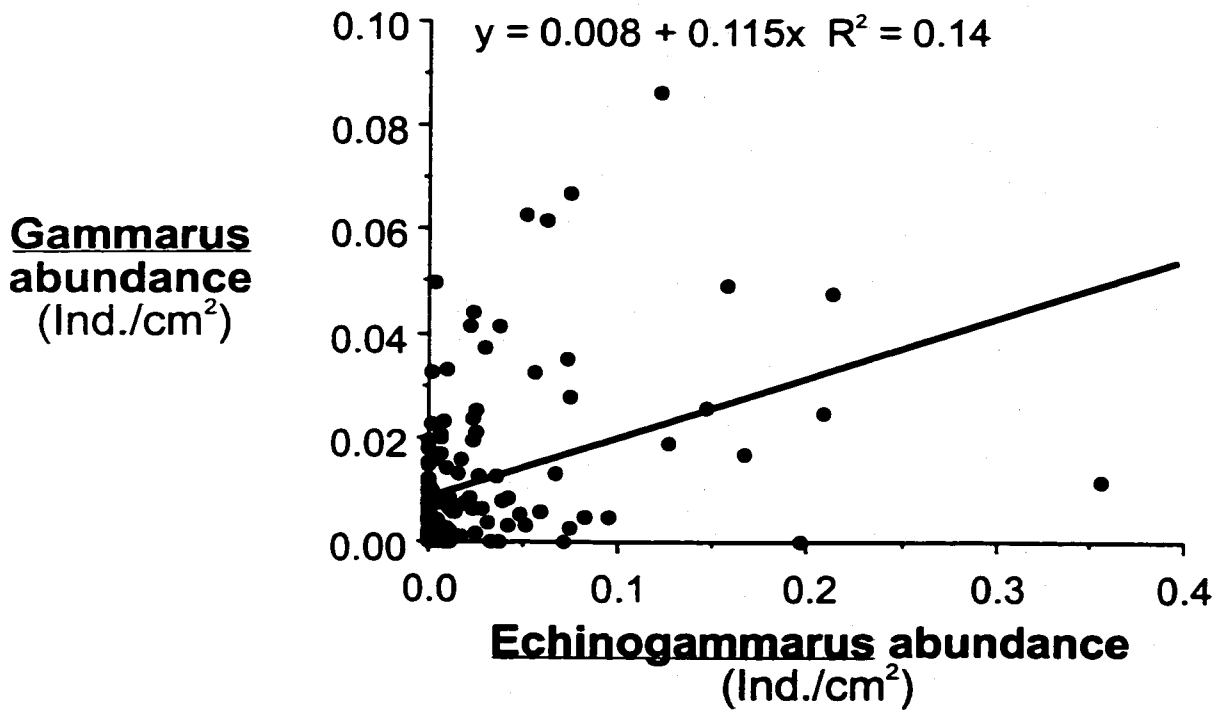
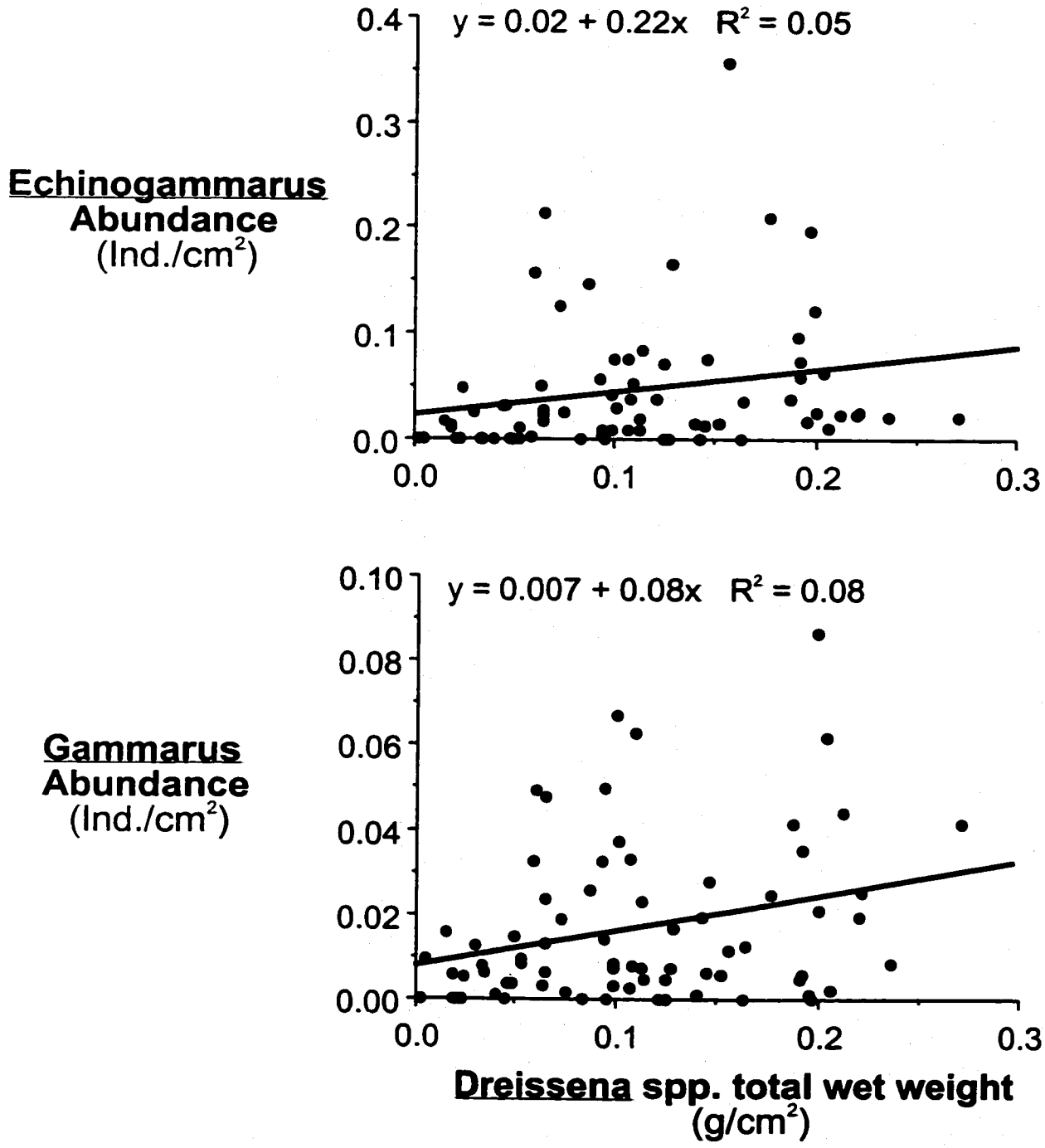


Figure 5. Relationship between abundance of Echinogammarus ischnus (Ind./cm^2) and abundance of Gammarus fasciatus (Ind./cm^2) on all four substrate types from the July and August experiments. Note change in y-axis scale.

Figure 6. Relationship between abundance of Echinogammarus ischnus (Ind./cm^2), and abundance of Gammarus fasciatus (Ind./cm^2) with total Dreissena total wet weight (g/cm^2). Note difference in y-axis scales.


y = 0.02 + 0.22x R² = 0.05
Echinogammarus Abundance (Ind./cm²)
0.4
0.3
0.2
0.1
0.0
0.0
0.1
0.2
0.3
y = 0.007 + 0.08x R² = 0.08
Gammarus Abundance (Ind./cm²)
0.10
0.08
0.06
0.04
0.02
0.00
0.0
0.1
0.2
0.3
Dreissena spp. total wet weight (g/cm²)

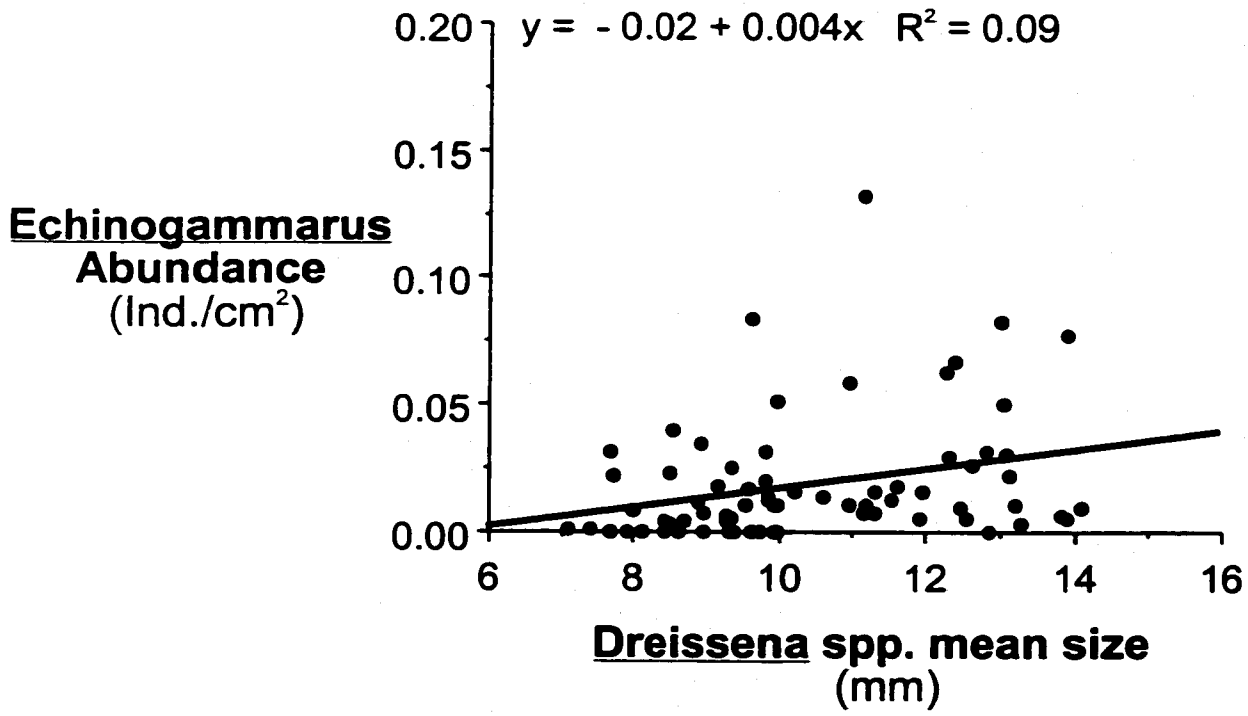


Figure 7. Relationship between abundance of Echinogammarus ischnus (Ind./cm^2) and mean mussel length (mm) on both Dreissena-encrusted treatments for July and August.

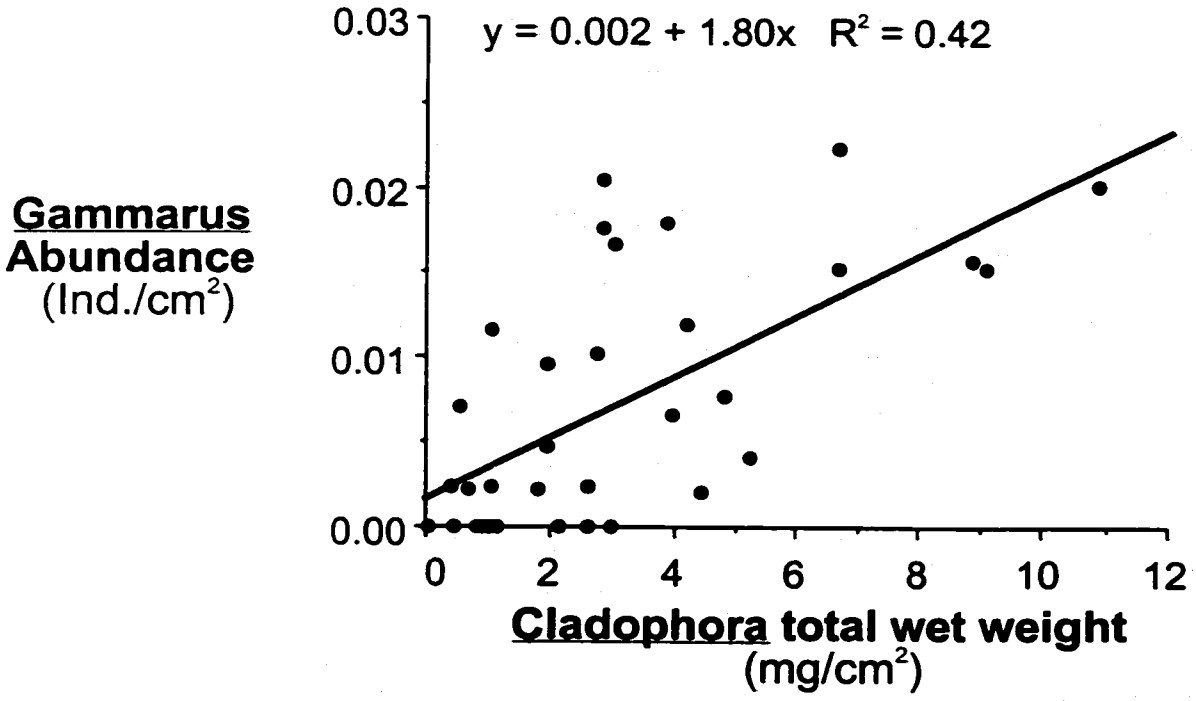


Figure 8. Relationship between abundance of Gammarus fasciatus (Ind./cm^2) and Cladophora total wet weight (g/cm^2) for July and August.

Table 1. Mean ± one standard error of biomass encrusted on experimental rocks, and mean mussel size ± standard error, for the July and August experiments.

	July 1998	August 1998
Substrate	(mg/cm^2) ± S.E.	(mg/cm^2) ± S.E.
Cladophora glomerata on Cladophora-encrusted rocks	5.0 ± 0.6	1.0 ± 0.2
C. glomerata on Dreissena-encrusted rocks	2.0 ± 0.2	1.0 ± 0.2
C. glomerata on Dreissena + Cladophora-encrusted rocks	2.0 ± 0.1	2.0 ± 0.3
Dreissena spp. on Dreissena-encrusted rocks	168.0 ± 12.0	85.0 ± 11.0
Dreissena spp. on Dreissena + Cladophora-encrusted rocks	80.0 ± 11.0	100.0 ± 16.0
Mean mussel size (mm)	10.2 ± 0.3	10.0 ± 0.2

Table 2. Multiple analysis of variance for abundance of Echinogammarus ischnus and Gammarus fasciatus (amphipod abundance corrected for controls, divided by rock area and log X + 1 transformed) for the July and August experiments. Treatment, date and depth are independent categorical variables.

Test	Species	Independent variable	Wilk's Lambda	df	F-ratio	P
Multivariate		Treatment	0.495	6, 240	16.87	< 0.001
		Date	0.700	2, 120	25.76	< 0.001
		Depth	0.612	8, 240	8.35	< 0.001
		Treatment × Depth	0.639	24, 240	2.51	< 0.001
		Treatment × Date	0.773	6, 240	5.51	< 0.001
Univariate	Echinogammarus	Treatment		3, 121	20.65	< 0.001
		Date		1, 121	17.72	< 0.001
		Depth		4, 121	9.96	< 0.001
		Treatment × Depth		12, 121	2.84	0.002
		Treatment × Date		3, 121	5.63	0.001
	Gammarus	Treatment		3, 121	26.04	< 0.001
		Date		1, 121	19.21	< 0.001
		Depth		4, 121	11.00	< 0.001
		Treatment × Depth		12, 121	2.92	0.001
		Treatment × Date		3, 121	3.87	0.011

Table 3. Regression analyses on abundance of Echinogammarus ischnus (amphipod abundance corrected by rock area) for the July and August experiments examining effects of rock area, encrusted biomass (g/cm^2), and mean mussel size (mm) encrusted on Dreissena treatments.

Effect	Source	df	F-ratio	P
Bare rock area	Regression Residual	1 35	0.99	0.328
Cladophora-encrusted rock area	Regression Residual	1 32	0.18	0.677
Cladophora-encrusted biomass	Regression Residual	1 32	0.24	0.627
Dreissena-encrusted rock area	Regression Residual	1 72	<0.01	0.994
Dreissena-encrusted biomass	Regression Residual	1 72	4.00	0.049
Mean mussel size	Regression Residual	1 72	6.95	0.010

Table 4. Regression analyses on abundance of Gammarus fasciatus (amphipod abundance corrected by rock area) for the July and August experiments examining effects of rock area, encrusted biomass (g/cm^2), and mean mussel size (mm) encrusted on Dreissena treatments.

Effect	Source	df	F-ratio	P
Bare rock area	Regression Residual	1 35	1.36	0.251
Cladophora-encrusted rock area	Regression Residual	1 32	3.62	0.067
Cladophora-encrusted biomass	Regression Residual	1 32	22.84	<0.001
Dreissena-encrusted rock area	Regression Residual	1 72	1.79	0.185
Dreissena-encrusted biomass	Regression Residual	1 72	6.34	0.014
Mean mussel size	Regression Residual	1 72	2.10	0.152

Conclusion

Conclusion

In this thesis, I attempted to explore habitat preferences of the Ponto-Caspian amphipod Echinogammarus ischnus and the Laurentian Great Lakes amphipod Gammarus fasciatus in laboratory and field experiments. I verified the existence of Echinogammarus in Lake Erie in 1994, a year prior to its initial discovery by Witt *et al.* (1997). Echinogammarus was found in three locations in Lake Erie during 1994: Middle Sister, East Sister and Pelee Islands. Its location and abundance (Figures 1 and 2; Chapter 1) suggests that the possible inoculation site of this amphipod occurred in the western basin of the lake. Size distributions (Figure 3; Chapter 1) demonstrate that Echinogammarus was a fully reproducing population with different generations during June 1994. Thus, I postulate that Echinogammarus invaded Lake Erie no later than 1993.

Throughout this thesis, I demonstrated that both species have a high affinity for complex substrates (e.g. Cladophora- or Dreissena-encrusted rocks) over less complex ones (bare rock), although the nature of substrate selection was greater for one species than the other. Echinogammarus abundance was always greater on Dreissena-encrusted rocks than on bare rocks or Cladophora-encrusted rocks, while Gammarus abundance was similar on Cladophora- and Dreissena-encrusted rocks, but always greater than on bare rock. Both species also selected complex substrates both in early (June and July) and late summer (August).

I attempted to experimentally explore replacement of Gammarus by Echinogammarus, which is apparently occurring in Lake Erie, but did not detect any interaction in the mixed species laboratory treatments after 24-hours (Chapter 2). In the field experiment, I detected no evidence of competition between amphipod species, but

rather densities were weakly positively correlated after 72 hours (Chapter 3). However, amphipod densities on encrusted, natural substrates displayed weak evidence of competition, as the abundance of one species corresponded inversely with the abundance of the other (Chapter 1). Thus, interactions between these two species are neutral over short time periods (24 hours; Chapter 2), commensal over brief time periods (72 hours; Chapter 3), and negative over longer time periods (Chapter 1), due to abundance patterns of both species.

Finally, I attempted to discern relationships between colonization and occupation of rocky substrates and habitat quality. Although patterns were noticeable, they tended to vary in both laboratory and field experiments, as well as over time. Rock size effects on amphipod abundance varied by species. In the laboratory and field experiments, Echinogammarus and Gammarus did not prefer smaller bare rocks to larger ones. Rocks encrusted with Cladophora had no effect on abundance of either species in the laboratory or field experiments, but Echinogammarus abundance was higher on larger Cladophora-encrusted rocks than on smaller ones during the temporal survey. Echinogammarus abundance was higher on smaller Dreissena-encrusted rocks in Chapter 1, yet did not display this pattern during the laboratory or field experiments

Gammarus abundance varied with Dreissena-encrusted biomass between the laboratory, field, and temporal study. In the laboratory experiment, it exhibited no relationship with Dreissena-encrusted biomass, but in the field experiment its abundance increased with increasing biomass (Figure 6; Chapter 3). In the temporal study, it had an inverse relationship in abundance with increasing Dreissena biomass (Figure 9; Chapter 1). This is contrary to many studies that reported high Gammarus abundance on

Dreissena substrate. Thus, Gammarus may be affected by living within Dreissena clumps over long time periods in the presence of Echinogammarus.

Echinogammarus abundance was positively correlated with Dreissena-encrusted biomass in both laboratory and field experiments. Thus, Echinogammarus preferentially exploits Dreissena, apparently due to co-evolution of these species in Eurasia. In this regard, introduction and spread of Dreissena in the Great Lakes appears to have facilitated colonization, establishment and dispersal of Echinogammarus in a manner consistent with Simberloff and Von Holle's (1999) 'invasional meltdown' hypothesis.

Due to the successful establishment of Dreissena spp. within the Great Lakes, it may have led to the subsequent invasion of Echinogammarus, as food resources and habitat were readily available for the amphipod. High abundances of Gammarus observed prior to the invasion of Echinogammarus decreased as the new amphipod established, possibly due to Echinogammarus' higher affinity for Dreissena substrate. This affinity, coupled with Echinogammarus' aggressive nature may lead to the replacement of amphipod species among Dreissena substrate.

Finally, the establishment of Echinogammarus and its high affinity for Dreissena may lead to additional introductions by other amphipod species such as Dikerogammarus, Pontogammarus, Obesogammarus and Corophium, as they have been reported to live in close association with one another and with Dreissena in their native range, accentuating further the 'invasional meltdown' hypothesis.

References

Barrett, S.C.H., and Richardson, B.J. 1986. Genetic attributes of invading species. Ecology of Biological Invasions. Cambridge University Press. Cambridge. pp. 21-33.

Barton, D.R., and Hynes, H.B.N. 1976. The distribution of amphipoda and isopoda on the exposed shores of the Great Lakes. *J. Great Lakes Res.* **2**:207-214.

Beckett, D.C., Lewis, P.A., and Green, J.H. 1998. Where have all the Crangonyx gone? The disappearance of the amphipod Crangonyx pseudogracilis, and subsequent appearance of Gammarus nr. fasciatus, in the Ohio River. *Am. Mid. Nat.* **139**:201-209.

Bially, A., and MacIsaac, H.J. 2000. Fouling mussels (Dreissena spp.) colonize soft sediments in Lake Erie and facilitate benthic invertebrates. *Freshwat. Biol.* **43**: 85-97.

bij de Vaate, A., and Klink, A.G. 1995. Dikerogammarus villosus Sowinisky (Crustacea: Gammaridae) a new immigrant in the Dutch part of the lower Rhine. *Lauterbornia H.* **20**: 51-54.

Bocsor, J.G., and Judd, J.H. 1972. Effect of paper plant pollution and subsequent abatement on a littoral macroinvertebrate community in Lake Ontario: preliminary survey. *Proc. 15th Conf. Great Lakes Res. 1972*:21-34.

Botts, P.S., Patterson, B.A., and Schlosser, D.W. 1996. Zebra mussel effects on benthic invertebrates: physical or biotic? *J. N. Am. Benthol. Soc.* **15**:179-184.

Bruner, K.A., Fisher, S.W., and Landrum, P.F. 1994. The role of the zebra mussel, (Dreissena polymorpha), in contaminant cycling: II. Zebra mussel contaminant accumulation from algae and suspended particles, and transfer to the benthic invertebrate, Gammarus fasciatus. *J. Great Lakes Res.* **20**:735-750.

Burkart, G.A. 1999. Zebra mussel mediation of habitat use by native and exotic amphipods: importance of food availability and predation risk. M. Sc. *Wright State University.*

Carlton, J.T., and Geller, J.B. 1993. Ecological roulette: the global transport of nonindigenous marine organisms. *Science* **261**:78-82.

Carlton, J.T. 1996. Biological invasions and cryptogenic species. *Ecology* **77**:1653-1655.

Chapman, J.W. 1988. Invasions of the Northeast Pacific by Asian and Atlantic Gammaridean amphipod crustaceans, including a new species of Corophium. *J. Crus. Bio.* **8**: 364-382.

Chase, F.A. Jr., Mackin, J.G., Hubricht, L., Banner, A.H., Hobbs, H.H. Jr. 1959. Malacostraca. In *Freshwater Biology, 2nd Edition*, ed. W.T. Edmondson, pp. 869-901. New York: John Wiley & Sons, Inc.

Ciborowski, J.J.H. 1992. Estimating processing time of stream benthic samples. *Hydrobiologia* **222**: 101-108.

Clemens, H.P. 1950. Life cycle and ecology of Gammarus fasciatus Say. The Ohio State University. pg. 1-63.

Cohen, A.N., and Carlton, J.T. 1998. Accelerating invasion rate in a highly invaded estuary. *Science* **279**:555-558.

Crawley, M.J. 1986. The population biology of invaders. *Phil. Trans. R. Soc. Lond. B* **314**: 711-731.

Dahl, J.A., Graham, D.M., Dermott, R., Johannsson, O.E., Millard, E.S., and Myles, D.D. 1995. Lake Erie 1993, western, west central and eastern basins: change in trophic status, and assessment of the abundance, biomass and production of the lower trophic levels. *Can. Tech. Rep. Fish. Aquat. Sci.* 2070.

Dediu, I.I. 1980. Amphipods of fresh and brackish waters of the southwestern USSR. Shtiintsa Publishers, Kishinev. [In Russian]

Delong, M.D., Summers, R.B., and Thorp, J.H. 1993. Influence of food type on the growth of riverine amphipod, Gammarus fasciatus. *Can. J. Fish. Aquat. Sci.* **50**:1891-1896.

den Hartog, C., van den Brink, F.W.B., and van der Velde, G. 1992. Why was the invasion of the River Rhine by Corophium curvispinum and Corbicula species so successful? *J. Nat. His.* **26**: 1121-1129.

Dermott, R., Mitchell, J., Murray, I., and Fear, E. 1993. Biomass and production of zebra mussels (Dreissena polymorpha) in shallow waters of Northeastern Lake Erie. *In* Zebra Mussels: Biology, Impacts and Control. Lewis Publishers. *Edited by* T.F. Nalepa and D.W. Schlosser, Lewis Publishers, Boca Raton, Fla. pp. 399-413.

Dermott, R., Witt, J., Um, Y.M., and González, M. 1998. Distribution of the Ponto-Caspian amphipod Echinogammarus ischnus in the Great Lakes and replacement of native Gammarus fasciatus. *J. Great Lakes Res.* **24**:442-452.

Dick, J.T.A., and Elwood, R.W. 1996. Effects of natural variation in sex ratio and habitat structure of mate-guarding decisions in amphipods (Crustacea). *Behaviour* **133**:985-996.

Dubs, D.O.L, and Corkum, L.D. 1996. Behavioral interactions between round gobies (Neogobius melanostomus) and mottled sculpins (Cottus bairdi). *J. Great Lakes Res.* **22**: 838-844.

Dunn, O.J., and Clark, V.A. 1974. Applied statistics: analysis of variance and regression. John Wiley & Sons. p. 339.

Dusoge, K. 1966. Composition and interrelations between macrofauna living on stones in the littoral of Mikolajskie Lake. *Eko. Pol.-Ser. A* **39**:755-763.

Edlund, M.B., Taylor, C.M., Schelske, C.L., and Stoermer, E.F. 2000. Thalassiosira baltica (Grunow) Ostenfeld (Bacillariophyta), a new exotic species in the Great Lakes. *Can. J. Fish. Aquat. Sci.* **57**:610-615.

Ehrlich, P.R. 1989. Attributes of invaders and the invading processes: vertebrates. biological invasions: a global perspective. John Wiley & Sons Ltd. pp. 315-328.

Elton, C.S. 1958. The ecology of invasions by animals and plants. London: Methuen.

Enserink, M. 1999. Biological invaders sweep in. *Science* **285**:1834-1836

González, M., and Downing, A. 1999. Mechanisms underlying amphipod responses to zebra mussel (Dreissena polymorpha) invasion and implications for fish-amphipod interactions. *Can. J. Fish. Aquat. Sci.* **56**:679-685.

Goodwin, B.J., McAllister, A.J., and Fahrig, L. 1999. Predicting invasiveness of plant species based on biological information. *Conserv. Biol.* **13**:422-426.

Griffiths, R.W. 1993. Effects of zebra mussels (Dreissena polymorpha) on the benthic fauna of Lake St. Clair. *In* Zebra Mussels: Biology, Impacts and Control. Lewis Publishers. *Edited by* T.F. Nalepa and D.W. Schlosser, Lewis Publishers, Boca Raton, Fla. pp. 415-437.

Grigorovich, I.A., and MacIsaac, H.J. 1999. First record of Corophium mucronatum Sars (Crustacea: Amphipoda) in the Great Lakes. *J. Great Lakes Res.* **25**:401-405.

Hebert, P.D., Muncaster, B.W., and Mackie, G.L. 1989. Ecological and genetic studies on Dreissena polymorpha (Pallas): a new mollusc in the Great Lakes. *Can. J. Fish. Aquat. Sci.* **46**:1587-1591.

Jaźdźewski, K. 1980. Range extensions of some Gammaridean species in European inland waters caused by human activity. *Crustaceana, Suppl.* **6**:84-107.

Jaźdźewski, K., and Konopacka, A. 1993. Survey and distribution of Crustacea malacostraca in Poland. *Crustaceana* **65**:176-191.

Jones, M. 1991. Marine organisms transported in ballast water: a review of the Australian scientific position. Bureau of Rural Resources Bulletin No. 11, Australian Government Publishing Service, Canberra.

Jude, D.J., and Deboe, S.F. 1996. Possible impact of gobies and other introduced species on habitat restoration efforts. *Can. J. Fish. Aquat. Sci.* **53** (SUPPL. 1):136-141.

Jude, D.J., Reider, R.H, and Smith, G.R. 1992. Establishment of Gobiidae in the Great Lakes basin. *Can. J. Fish. Aquat. Sci.* **49**:416-421.

Köhn, J., and Waterstraat, A. 1990. The amphipod fauna of Lake Kummerow (Mecklenburg, German Democratic Republic) with reference to Echinogammarus ischnus Stebbing, 1899. *Crustaceana* **58**:74-82.

Konopacka, A., and Jesionowska, K. 1995. Life history of Echinogammarus ischnus (Stebbing, 1898) (Amphipoda) from artificially heated Licheńskie Lake (Poland). *Crustaceana* **68**:341-349.

Kuhns, L.A., and Berg, M.B. 1999. Benthic invertebrate community responses to round goby (Neogobius melanostomus) and zebra mussel (Dreissena polymorpha) invasion in southern Lake Michigan. *J. Great Lakes Res.* **25**:910-917.

Lauzon, J.D., and MacIsaac, H.J. 1997. Biological invasions: are they dependent on disturbance? *Environ. Rev.* **5**: 131-144.

Lodge, D.M. 1993. Biological invasions: lessons for ecology. *Trend Ecol. Evol.* **8**:133-137.

Lodge, D.M., Stein, R.A., Brown, K.M., Covich, A.P., Brönmark, C., Garvey, J.E., and Klosiewski, S.P. 1998. Predicting impact of freshwater exotic species on native biodiversity: challenges in spatial scaling. *Aust. Ecol.* **23**:53-67.

MacIsaac, H.J. 1996a. Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. *Amer. Zool.* **36**: 287-299.

MacIsaac, H.J. 1996b. Population structure of an introduced species (Dreissena polymorpha) along a wave-swept disturbance gradient. *Oecologia.* **105**:484-492.

MacIsaac, H.J., Grigorovich, I.A., Hoyle, J.A., Yan, N.D., and Panov, V.E. 1999. Invasion of Lake Ontario by the Ponto-Caspian predatory cladoceran Cercopagis pengoi. *Can. J. Fish. Aquat. Sci.* **56**:1-5.

May, B., and Marsden, J.E. 1992. Genetic identification and implications of another invasive species of Dreissenid mussel in the Great Lakes. *Can. J. Fish. Aquat. Sci.* **49**:1501-1506.

Mills, E.L., Leach, J.H., Carlton, J.T., and Secor, C.L. 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. *J. Great Lakes Res.* **19**:1-54.

Mordukhai-Boltovskoi, F.D. 1958. Process of the distribution of the Caspian fauna during modern epoch. *In* Problems of terrestrial zoogeography. Izdatelstvo L'vovskogo universiteta, Lvov, the Ukrainian SSR. pp. 173-182. [In Russian].

Mordukhai-Boltovskoi, F.D. 1964. Caspian fauna beyond the Caspian Sea. *Int. Revue. ges. Hydrobiol.* **49**:139-176.

Pimentel, D., Lach, L., Zuniga, R., and Morrison, D. 2000. Environmental and economic costs associated with non-indigenous species in the United States. *Bioscience*. **50**:53-65.

Pinkster, S. 1993. A revision of the genus Echinogammarus Stebbing, 1899 with some notes on related genera (Crustacea, Amphipoda). *Mem.Del Mus. Civ. Di Stor. Nat.* Pg. 1-185.

Rajagopal, S., van der Velde, G., Paffen, B.G.P., and bij de Vaate, A. 1997. Ecology and impact of exotic amphipod, Corophium curvispinum Sars, 1895 (Crustacea: Amphipoda), in the River Rhine and Meuse. Report (No.) of the project "Ecological rehabilitation of rivers Rhine and Meuse". Institute for Inland Water Management and Waste Water Treatment. (The Netherlands).

Ricciardi, A., Whoriskey, F.G., and Rasmussen, J.B. 1997. The role of the zebra mussels (Dreissena polymorpha) in structuring macroinvertebrate communities on hard substrata. *Can. J. Fish. Aquat. Sci.* **54**:2596-2608.

Ricciardi, A., and Rasmussen, J.B. 1998. Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. *Can. J. Fish. Aquat. Sci.* **55**: 1759-1765.

Ricciardi, A., and MacIsaac, H.J. 2000. Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. *Trend Ecol. Evol.* **15**:62-65.

Ruiz, G.M, Carlton, J.T., Grosholz, E.D., and Hines, A.H. 1997. Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. *Amer. Zool.* **37**:621-632.

Shear, H. and Konasewich, D.E. 1975. Cladophora in the Great Lakes. Great Lakes Research Advisory Board, International Joint Commission. pg. 1-179.

Shorygin, A. 1952. The feeding and food-relationships of the fishes in the Caspian Sea (Acipenseridae, Cyprinidae, Gobiidae, Percidae and predatory Herrings). Moscow. Ed. Pistchepromizdat Pg. 1-268. [In Russian]

Simberloff, D., and Von Holle, B. 1999. Synergistic interactions of nonindigenous species: Invasional meltdown? *Biol. Invas.* **1**:21-32.

Stewart, T.W., and Haynes, J.H. 1994. Benthic macroinvertebrate communities of southwestern Lake Ontario follow invasion of Dreissena. *J. Great Lakes Res.* **20**:479-493.

Stewart, T.W., Miner, J.G., and Lowe, R.L. 1998a. Quantifying mechanisms for zebra mussel effects on benthic macroinvertebrates: organic matter production and shell-generated habitat. *J. N. Am. Benthol. Soc.* **17**:81-94.

Stewart, T.W., Miner, J.G., and Lowe, R.L. 1998b. An experimental analysis of crayfish (Orconectes rusticus) effects on a Dreissena-dominated benthic macroinvertebrate community in western Lake Erie. *Can. J. Fish. Aquat. Sci.* **55**:1043-1050.

Stewart, T.W., Miner, J.G., and Lowe, R.L. 1999. A field experiment to determine Dreissena and predator effects on zoobenthos in a nearshore, rocky habitat of western Lake Erie. *J. N. Am. Benthol. Soc.* **18**:488-498.

Strayer, D.L., Smith, L.C., and Hunter, D.C. 1998. Effects of the zebra mussel (Dreissena polymorpha) invasion on the macrobenthos of the freshwater tidal Hudson River. *Can. J. Zool.* **76**:419-425.

Summers, R.B., Delong, M.D., and Thorp, J.H. 1997. Ontogenetic and temporal shifts in the diet of the amphipod Gammarus fasciatus, in the Ohio River. *Am. Mid. Nat.* **137**:329-336.

Taft, C.E. 1975. "History of Cladophora in the Great Lakes." In: Cladophora in the Great Lakes. Great Lakes Research Advisory Board, International Joint Commission. pp. 9-16.

United States Coast Guard. 1993. Ballast water management for vessels entering the Great Lakes. 33-CFR Part 151.1510.

van den Brink, F.W.B., van der Velde, G., and bij de Vaate, A. 1991. Amphipod invasion on the Rhine. *Nature* **352**: 576.

van den Brink, F.W.B., van der Velde, G., and bij de Vaate, A. 1993. Ecological aspects, explosive range extension and impact of a mass invader, Corophium curvispinum Sars, 1895 (Crustacea: Amphipoda), in the Lower Rhine (The Netherlands). *Oecologia* **93**: 224-232.

Vermeij, G.J. 1996. An agenda for invasion biology. *Biol. Conser.* **78**: 3-9.

Weckel, A.L. 1907. The freshwater amphipods of North America. *Proc. U.S. Nat. Mus.* **32**:25-58.

Wells, H.G. 1904. The Food of the Gods.

Williamson, M., and Fitter, A. 1996. The varying success of invaders. *Ecology* **77**: 1661-1666.

Wisenden, P.A., and Bailey, R.C. 1995. Development of macroinvertebrate community structure associated with zebra mussels (Dreissena polymorpha) colonization of artificial substrates. *Can. J. Zool.* **73**:1438-1443.

Witt, J.D.S., Hebert, P.D.N., and Morton, W.B. 1997. Echinogammarus ischnus: another crustacean invader in the Laurentian Great Lakes basin. *Can. J. Fish. Aquat. Sci.* **54**:264-268.

Yemelianova, L.V. 1994. Gammarids of the littoral of the Dnieper Reservoirs. Naukova dumka, Kiev, Ukraine. Pg. 1-145. [In Russian]

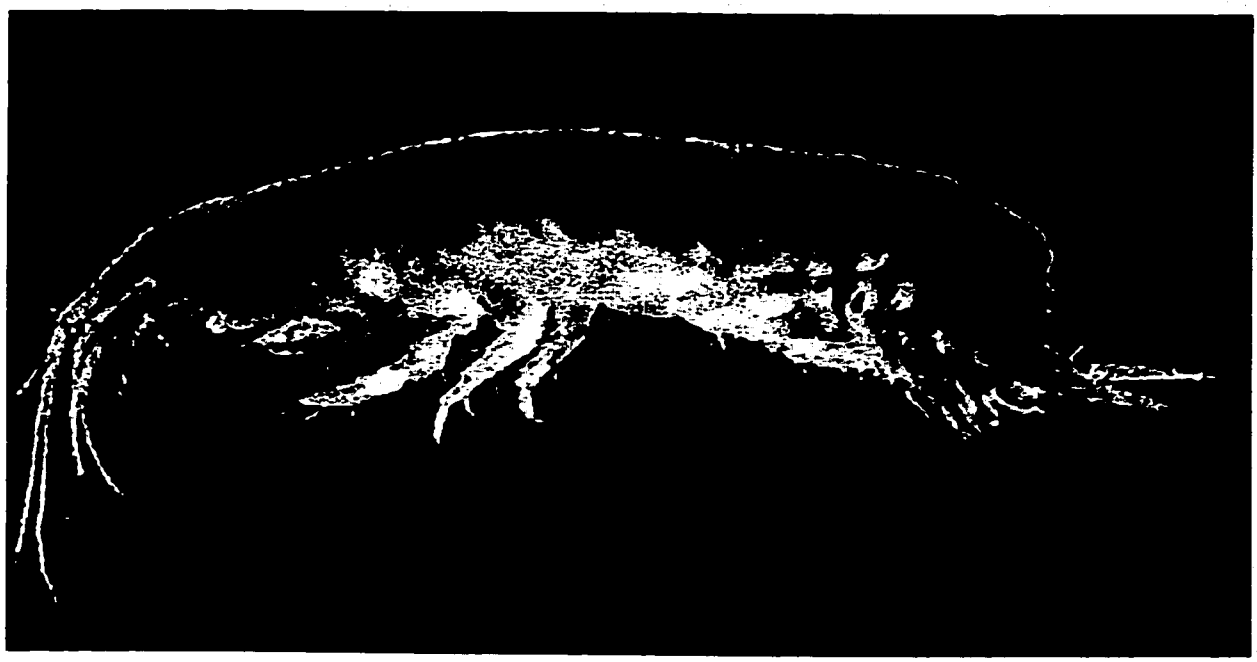
Zhang, F., and Dickman, M. 1999. Mid-ocean exchange of container vessel ballast water 1: seasonal factors affecting the transport of harmful diatoms and dinoflagellates. *Mar. Eco. Prog. Ser.* **176**: 243-251.

Appendix

Gammarus fasciatus

- Sexually dimorphic and reproduction is entirely sexual
- Body length of males (mature between 9.0 and 10.2 mm) longer than that of females (mature between 7.4 and 8.8 mm) and is more laterally compressed
- Copulation occurs after molting of the female
- Number of eggs produced per brood is related to size of females and ranges from 1 – 48 eggs (maximum of 75 from a female of 14.0 mm), average of 17 over the breeding season
- Two main breeding periods, one between late March and late June and the other in August and early October
- Incubation period of eggs is dependent on water temperature ranging from 7 – 22 days at temperature of 24 and 15 °C, respectively
- Immatures reach maturity after seven molts
- Omnivorous feeding habits, feeds on both living and dead plant and animal matter
- Approximate life span of about 8 months

Echinogammarus ischnus



- Sexually dimorphic and reproduction is entirely sexual
- Body length of males (up to 13 – 15 mm in natural habitat and up to 11 – 12 mm in invaded habitats) longer than that of females (up to 11 – 12 mm in natural habitat and up to 8 – 9 mm in invaded habitats)
- Copulation occurs after molting of the female
- Number of eggs produced per brood is related to size of females and ranges from 7 - 48 eggs (mean of 25) in natural habitat, and from 3 - 27 (mean of 10) in invaded habitats
- Two main breeding periods, one between March and June and the other in August and September, but extends until October
- Incubation period of eggs is dependent on water temperature ranging from 55 - 65 days at temperature of 20 - 21 °C, or 44 – 56 days at 23 - 24 °C
- 2 – 3 generations per year
- Omnivorous feeding habits, feeds on both living and dead plant and animal matter
- Approximate life span of about 8 months

Vita Auctoris

NAME:	Colin David Alexander van Overdijk
DATE OF BIRTH:	June 26, 1969
PLACE OF BIRTH:	Brantford, Ontario
EDUCATION:	North Park Collegiate and Vocational School Brantford, Ontario 1983 - 1988 University of Toronto Erindale College 1988 – 1992 Hons. B. Sc. University of Windsor 1998 – 2000 M. Sc. (Biology)